

The independent effects of forest amount, fragmentation,
and corridors on forest understory plant diversity

by

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Abstract

It is well documented that forest amount in the surrounding landscape increases understory plant species diversity in a forested site. However, the extent to which forest fragmentation and structural connectivity (wooded corridors linking forest patches) also influence understory plant diversity remains largely unknown due to repeated conflation of these with forest amount. Here, we test the independent effects of these three landscape variables (forest amount, forest fragmentation, and wooded corridors) on understory plant species diversity at 70 forested sites in eastern Ontario, Canada. Forest amount had large positive effects on richness and negative effects on species assemblage uniqueness. Forest fragmentation reduced species richness and species evenness, through negative effects on short-distance dispersers. Both forest amount and fragmentation had their maximum effects within 5 km of sample sites. Structural connectivity did not affect species richness of forest understory plants but reduced both species evenness and species assemblage uniqueness. The results demonstrate that maximizing forest amount is of primary importance for conserving forest plant species diversity. Where a choice for forest is available, forest restoration should occur in sites adjacent to existing forest. Finally, increasing structural connectivity is not a viable strategy for maintaining forest understory plant communities.

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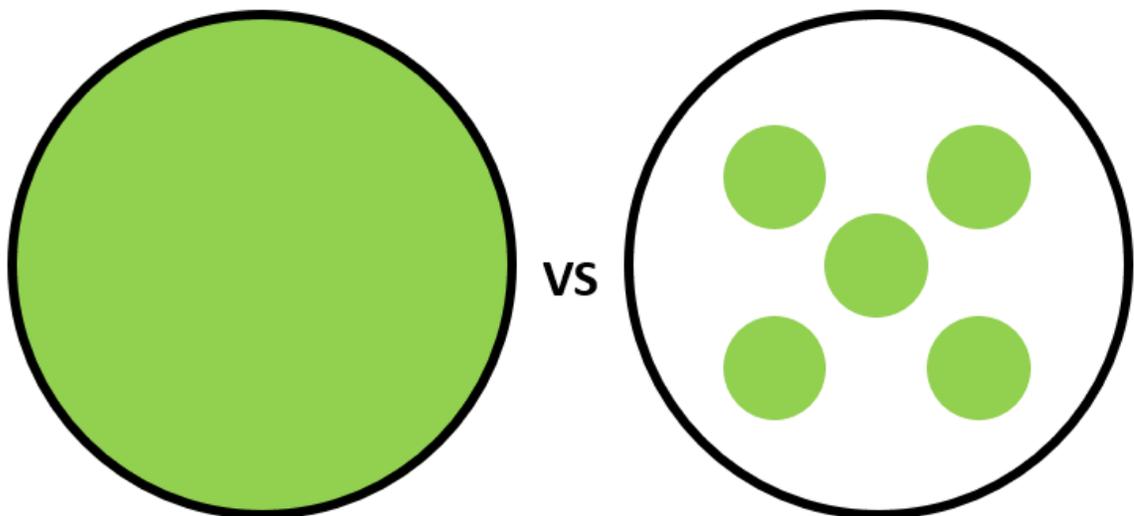
Introduction

Habitat loss is a main driver of species extinctions (Sinclair et al., 1995). The widespread expansion of human activity has reduced the area of natural habitat available to species and directly caused a reduction in species diversity (Pimm and Raven, 2000). These effects are assumed to follow the species-area relationship (SAR), one of the few ubiquitous trends in ecology (Lawton, 1999). As landscapes lose habitat, they contain a less diverse species pool because the size of each population is lower, increasing the likelihood of species extinctions (Fahrig, 2013, Lawton, 1999).

Habitat loss remains a main driver of species extirpations when analyzing effects on forest understory plant species (Brook, Sodhi, and Ng, 2003). Past studies have found that the amount of forest in the surrounding landscape is a strong driver of site-scale forest understory species richness (Giam et al., 2010; Püttker et al., 2020). This trend is caused by habitat loss decreasing the carrying capacity of the landscape, which leads to more extirpation in the landscape since smaller populations will be more stable (Tschardt et al. 2012). The heterogeneity in the landscape's environment should decrease with forest loss because less habitat area will by chance capture less microhabitats in the landscape (Kallimanis et al. 2008), contributing further to this decrease in species richness. Furthermore, because different species have different sensitivities to forest loss, landscape-scale forest amount also affects local species composition of forest understory plants (Benchimol et al., 2017).

The fragmentation of forest into more, smaller patches may also affect species richness of understory plant populations. However, there is little clear empirical support for an effect of forest fragmentation, independent of forest amount, on understory plant

diversity. Many past studies have found that landscape-scale forest loss and fragmentation together can reduce plant species diversity (Haddad et al., 2015). Effects of forest fragmentation itself, independent of forest loss (fragmentation per se; Fahrig 2003), are less clear because many studies of the effects of forest fragmentation on plants conflate forest amount and fragmentation (see Fahrig 2003 for examples of this conflation). This conflation leads to uninterpretable results regarding the effects of fragmentation (Figure 1) (Wang et al., 2014), because when conflation is present it is not known if observed effects on species richness are caused by a change in habitat amount or habitat patchiness.



Fragmented Landscapes Also Tend to Have Less Habitat (Conflation)

Figure 1. Illustration of conflation of habitat amount and fragmentation in many of the past studies on fragmentation, which compared a continuously forested landscape to a landscape (or landscapes) with habitat divided into many patches. Forest patches are green circles and large black circles are landscape units. With this design there is no way to know whether a difference in species richness between the two landscapes is caused by the difference in habitat amount or in habitat subdivision (i.e. change in fragmentation).

Patch-scale studies also conflate habitat loss and fragmentation effects (Fahrig 2003). These include many studies of forest understory plant species' responses to patch size or distance to the nearest patch (patch isolation) that take these as indices of habitat fragmentation (e.g. Benítez-Malvido and Martínez-Ramos, 2003; Ross, Fox, and Fox, 2002, Jules, 1998). This conflates habitat amount and fragmentation because small patches contain less habitat than large patches, and more isolated patches have less habitat in their immediate surroundings. Therefore, studies that interpret negative effects of fragmentation from lower species richness in smaller, more isolated patches do not provide evidence of effects of fragmentation.

Conflation between habitat amount and fragmentation can be avoided by selecting sites that have a low correlation between fragmentation and habitat amount at a landscape scale (Figure 2; see also Pasher et al., 2013). Habitat amount and fragmentation can then be assessed to determine their relative effects (Smith et al., 2009; Wang et al., 2014; Villard and Metzger, 2013). Any correlation not controlled for through site selection can then be controlled for statistically using multiple regression (Smith et al., 2009). Two recent studies (Püttker et al., 2020; Lehtilä, Vinter, and Dinnetz, 2020) tested the independent effect of fragmentation and forest amount on forest understory plant species richness simultaneously. These studies both found negative effects of fragmentation on forest understory plant species richness (Püttker et al., 2020, Lehtilä, Vinter, and Dinnetz, 2020).

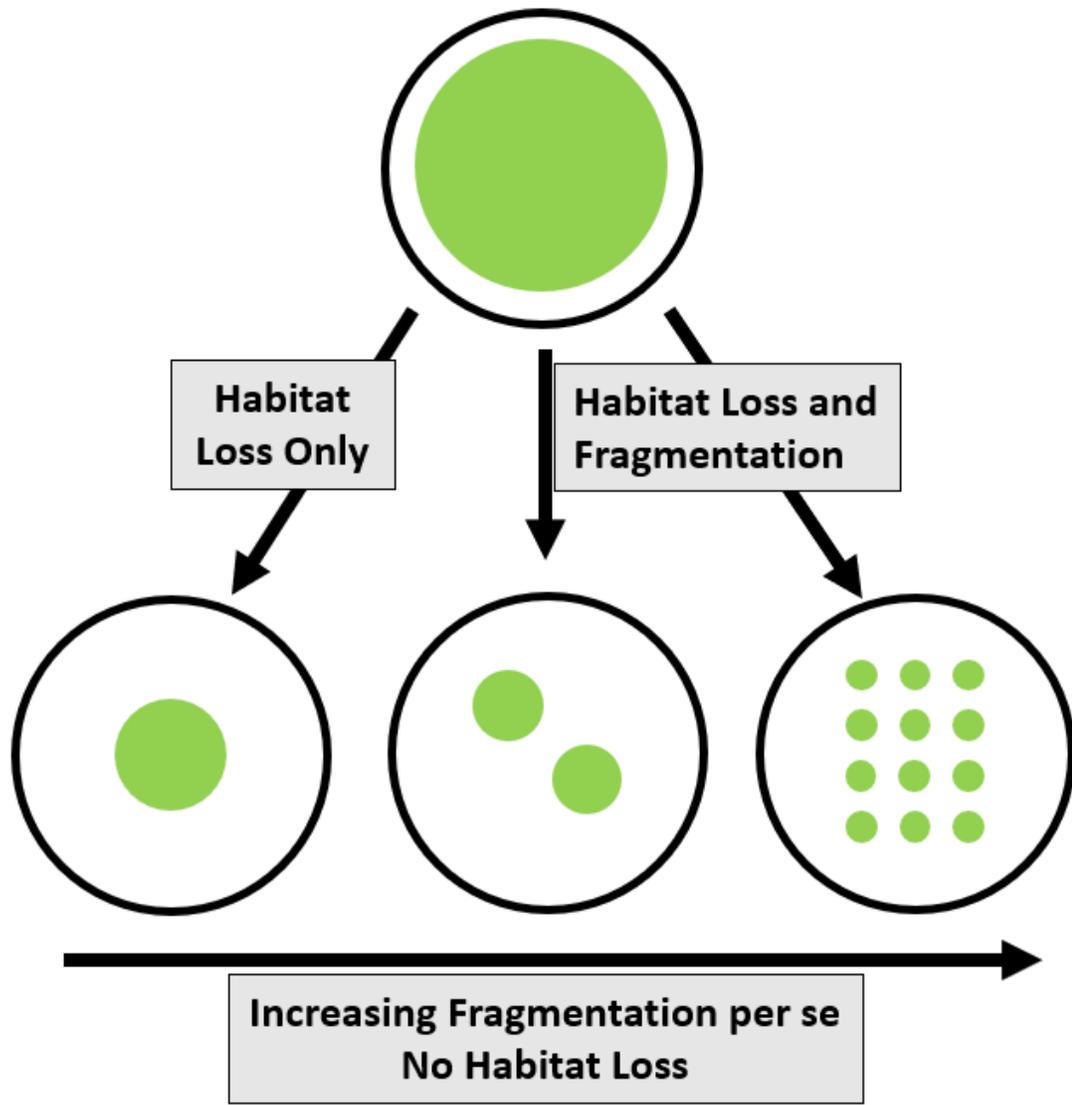


Figure 2. Illustration of habitat fragmentation per se, as distinct from habitat loss. Habitat is green circles and large black circles are landscape units. Fragmentation per se is the division of a given amount of habitat into more, smaller patches. Fragmentation is a change in habitat pattern, increasing habitat patchiness.

There are reasons to expect negative effects of forest fragmentation on understory plant richness when controlling for the effects of forest amount. A potential negative consequence of fragmentation for forest understory plants is the higher edge density in a

more fragmented landscape, which reduces the total amount of interior forest in the landscape. Landscapes with more patches of forest (for the same amount of forest) have more edge and less interior forest, resulting in less habitat for these forest interior species. Negative landscape-scale edge effects brought on by fragmentation could decrease species richness or alter species assemblages by decreasing the proportion of forest interior specialists at a forest site.

The increased edge density caused by fragmentation could also alter species assemblages by promoting the invasion of non-native species into forest interiors. Since non-native species are often abundant in forest edges (Cadotte and Lovett-Doust, 2001), non-native species could be provided more habitat when the landscape's forest is fragmented into many patches. Since non-native species can spill over into forest interiors from edges (Yates, Levia, and Williams, 2004), fragmentation could potentially promote the colonization of forests by non-native species that are dominant in edges. If this is true, we might expect the proportional richness of non-native species to increase with forest fragmentation.

Edge density could affect seed mortality by increasing likelihood of seeds landing in inhospitable matrix habitat (Devlaeminck, Bossuyt, and Hermy, 2005), with particularly strong negative effects on short distance dispersers. Forest plant species often disperse outside of patches into an inhospitable matrix (Devlaeminck, Bossuyt, and Hermy, 2005), where they are unable to germinate and grow. With more fragmentation in the landscape, dispersal outside of patches into the matrix should be more likely, because the landscape will have more edges where seeds can disperse outside of patches into the matrix. We speculate that negative edge effects on dispersal mortality are likely to occur

for species with seeds that are unable to cross gaps between forest patches. If this is true, we expect the proportion of short distance dispersers to decrease with fragmentation.

Conversely, we may predict positive effects of forest fragmentation on understory plant species richness because habitat heterogeneity within the forest may be higher in a more fragmented landscape. This is because environmental conditions tend to be clumped (Miller, Franklin, and Aspinall, 2007; Kim and Shin, 2016) and when habitat is divided into many patches it will be more evenly distributed through a landscape, which should capture more environmental variance (and therefore more niches) (Liu et al, 2018; Fahrig, 2020) (see Figure 4 prediction 2- for illustration of this mechanism). Landscapes with more variable environmental conditions and niches should conserve more specialist species with narrow niche requirements because they will contain a wider range of unique conditions that are needed to support these specialists (Liu et al, 2018). Past studies have supported this mechanism by finding that local plant species richness is positively correlated with landscape scale environmental heterogeneity (Costanza, Moody, and Peet, 2007). If these positive effects of heterogeneity are stronger than the negative effects of edge density on forest understory plants, then we would expect fragmentation to increase species richness.

Fragmentation can also positively alter the functional connectivity of landscapes by creating stepping stones that decrease the size of interpatch gaps. Functional connectivity directly describes a species' ability to move through the environment and relates not only to the continuity of habitat in the landscape, but also to a species' ability to navigate through the landscape to access habitat (Kimberley et al., 2021). Fragmentation could increase functional connectivity of the landscape by creating small

habitat patches throughout the landscape that could act as stepping stones, increasing the immigration rate by decreasing the size of interpatch gaps (Saura, Bodin, and Fortin, 2013). This potential for increased connectivity could also increase plant species richness in patchier landscapes.

Linear stretches of habitat connecting patches of the same habitat type ("corridors", Beier and Noss, 1998) are thought to reduce the negative effects of habitat loss and fragmentation by facilitating dispersal between patches (Tewksbury et al., 2002, Damschen et al., 2019). Past studies have found support for this mechanism for plants, with increasing structural connectivity via open-habitat corridors increasing plant species richness in patches of open habitat in a matrix of mature forest (Damschen et al., 2019). Other studies in the same system found that patches in connected landscapes have higher rates of pollination, seed dispersal, and fruit set (Tewksbury et al., 2002; Levey et al., 2005; Damschen et al., 2014).

Wooded corridors might similarly facilitate inter-patch movement of forest understory plants (Sitzia, 2007), which could result in higher species richness in connected forest sites. If animals tend to move between forest patches more often when wooded corridors are present, then corridors should facilitate the inter-patch movement of animal-dispersed seeds (Sitzia, 2007). Corridors could also act as drift fences for wind-dispersed seeds by intercepting them in the matrix. If these intercepted seeds can then grow to plants that produce more seeds in the corridors, the corridors effectively decrease the distance they need to travel to colonize new patches and decrease the proportion of seeds that fall in an inhospitable matrix (Oliveira et al, 2015; Bullock and Moy, 2004). Consistent with the stepping-stone idea, Roy & de Blois (2006) found that 83% of native

forest herbaceous species also occurred in hedgerows, and Wehling & Diekmann (2009) found similar reproductive success of five forest plants in hedgerows as in forest.

On the other hand, wooded corridors may not increase between-patch movement of forest interior understory plants. Although wooded corridors have been shown to provide habitat for forest plant species, Liira and Paal (2013) found that many of these are generalist and edge-dwelling plant species, and forest-interior species are often absent from sections of corridors that are far from forest patches (>15 m). This suggests that corridors may not be effective as stepping-stones for these forest interior species. If so, this would mean that for wooded corridors to facilitate dispersal of forest-understory specialists, they must facilitate the movement of seeds between patches in a single dispersal event, e.g. via animal dispersal. In this scenario, forest interior specialists that disperse short distances would be unlikely to benefit from wooded corridors, because they would be unable either to survive within corridors or disperse between patches in a single event (Travers, Härdtle, and Matthies, 2021). Nevertheless, these arguments remain speculative because studies of wooded corridors rarely test their effect on plant biodiversity within patches, but instead test diversity in the corridors themselves (Gilbert-Norton et al., 2010; Travers, Härdtle, and Matthies, 2021). For example, Roy & de Blois (2006) and Wehling & Diekmann (2009) both analyzed the similarities between corridors and forest patches but did not directly test how these corridors affecting diversity within forest patches.

As with fragmentation, studies evaluating the effects of corridors on biodiversity often conflate corridors and habitat amount (Figure 3). Corridors are habitat themselves (Beier and Noss, 1998), so any increase in diversity due to the addition of corridors could

be either due to an increase in connectivity or simply to the increase in habitat area represented by those corridors (Gilbert-Norton et al., 2010). No studies have controlled for this corridor-habitat conflation in forested systems, greatly hindering interpretation of the literature on the role of wooded corridors on forest plant dispersal (Davies and Pullin, 2007).

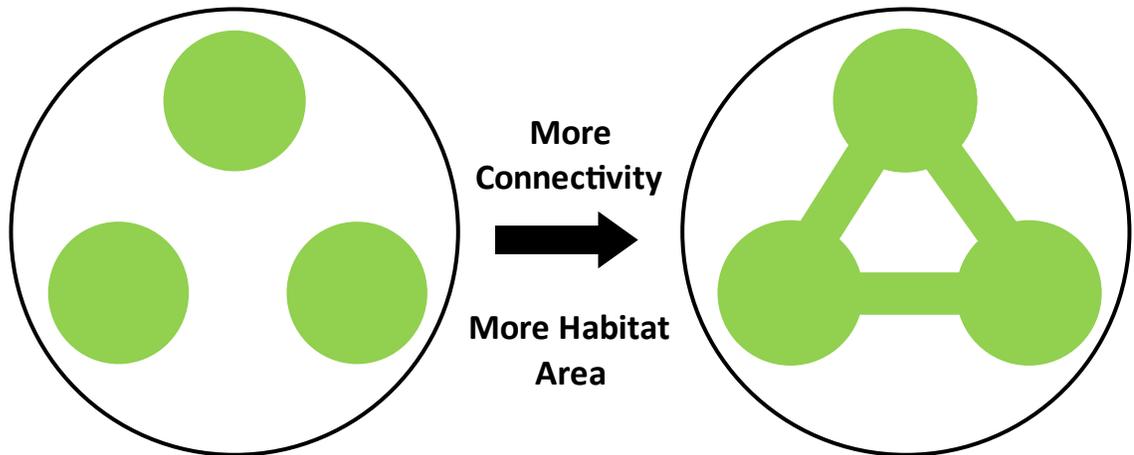


Figure 3. Illustration of conflation between corridor and habitat amount. Since corridors are habitat themselves, If two landscapes have the same area of habitat within patches, then the one with more corridors (and therefore more structural connectivity) will have more habitat area. This will inevitably lead to conflation between habitat amount and structural connectivity if this increased habitat is not accounted for statistically. Forest patches are green circles and corridors are green lines.

A landscape with more wooded corridors but the same total amount of wooded habitat could even have lower species richness of forest-interior plants because, for a given amount of forest, a landscape with more corridors will have less interior habitat. If the habitat that corridors provide is suboptimal for many species surveyed in forest interior sites, then landscapes with more corridors but the same total forest amount (including the corridors) will contain less habitat for the forest interior species (Liira and Paul, 2013; Deckers et al., 2004). This could lead to lower species richness at forest

interior sites in landscapes with more corridors than in landscapes with fewer corridors but the same total forest amount, as fewer forest interior species would be present in the landscape's species pool (Tschardt et al., 2012). Additionally, we might find a higher proportion of generalist and non-native species in highly connected forest sites if these species are more likely to disperse through corridors and to use them as habitat (Rosenberg, Noon, and Meslow, 1997; Travers, Härdtle, and Matthies, 2021; Resasco et al., 2014).

The arguments above predict changes in understory plant species richness in response to landscape structure, but the second major component of species diversity, namely species evenness, may not respond in the same way. For example, sample sites in landscapes with more interpatch dispersal may be more likely to be dominated by competitively dominant species (Mouquet and Loreau, 2003). This shift in dominance could lead to lower species evenness in sites in landscapes with more habitat, and with more corridors and patches for a given amount of habitat, as these are the landscapes where we expect more interpatch dispersal (Hillebrand, Bennett, and Cadotte, 2008). This could produce uneven species assemblages because of increased use of resources by competitively dominant species.

The landscape structure surrounding a forest site might also influence the contribution of that site to the beta diversity of the larger region. Population isolation and ecological drift should be higher in landscapes with less forest, fewer patches (Saura, Bodin, and Fortin, 2013), and fewer corridors connecting them (Rosenberg, Noon, and Meslow, 1997). This could lead to species pools in these landscapes that are less similar to the regional species pool than landscapes with more forest, more patches, and more

corridors. Past studies at the patch scale have found results consistent with this mechanism, finding more rare species in small patches than large ones (Deane and He, 2018; Wintle et al., 2019), though this remains to be tested at a landscape scale.

We tested these hypotheses by surveying forest understory plants in 70 forest sites, selected to represent independent gradients in forest amount, forest fragmentation (number of forest patches), and structural connectivity (proportion of other patches connected via corridors to the patch containing the survey site) in the surrounding landscapes. Specifically, we tested the following predictions:

1: Plant richness will increase with the amount of forest in the landscape surrounding the site.

2+: Plant species richness will decrease with forest fragmentation in the surrounding landscape due to increasing edge density.

2-: (alternate to prediction 2+) Plant species richness will increase with forest fragmentation in the surrounding landscape due to more dispersal and higher habitat heterogeneity.

3+: Forest sites in patches with higher connectivity will have higher plant species richness than forest sites in patches with lower connectivity (but the same total forest amount and number of patches), due to increased dispersal.

3- (alternate to prediction 3+): *Forest sites in patches with higher connectivity will have lower plant species richness than sites in patches with lower connectivity (but the same total forest amount and number of patches), due to the lower amount of forest interior habitat.*

4: *The effect size for the relationship between plant species richness and forest interior amount in the surrounding landscape will be larger than that for total forest cover in the surrounding landscape because plants sampled in forest interior sites are less common in forest edges than interiors.*

5: *When habitat amount is controlled for, forest sites in landscapes with more patches and in patches with higher connectivity will contain a higher proportion of forest generalist species, and a lower proportion of forest interior specialists.*

6: *When habitat amount is controlled for, forest sites in landscapes with more patches and in patches with higher connectivity will contain a higher proportion of non-native plant species.*

7: *When habitat amount is controlled for, forest sites in landscapes with more patches and in patches with lower connectivity will contain a lower proportion of short distance dispersers.*

8: Plant species evenness at forest sites will decline with forest amount, fragmentation, and structural connectivity.

9: The contribution of a forest site to regional beta diversity will decline with habitat amount, fragmentation, and number of corridors in the landscape surrounding the site.

<u>Prediction</u>	<u>Mechanism</u>		<u>Result:</u>	
1		More Forest = More Habitat		Higher Species Richness
2+, 3-, 5, 6, 7		More Patches & Structural Connectivity = More Edge; Less Interior		Lower Richness, Proportion of Forest Specialists & Proportion of Short Distance Dispersers Higher Proportion of Non-Native Species
2-		More Fragmentation per se = More Niches		Higher Species Richness
3+		More Structural Connectivity = More Dispersal		Higher Species Richness
8 & 9		Less Patches, Structural Connectivity & Forest = More Isolation		Higher Evenness & Beta Diversity

Figure 4. Illustration of mechanisms that underly our predictions. Forest patches are green circles, corridors are green lines, and sample sites are red crosses. Colours in the background of prediction 2- denote different environmental conditions (soil type, moisture, etc.) Arrows represent dispersal/movement. Red represents forest edge habitat and green forest interior habitat for predictions 2+, 3-, 5, 6, 7. Forest amount in a landscape includes the patches and corridors.

Methods

Study region and methods overview:

We conducted our study in Eastern Ontario, a region that was historically covered by nearly continuous forest but is now highly altered for agriculture and urban land use. This region's forests are typically composed of temperate deciduous or mixed forests (Bennett, 1987). Many of these forests are in patches surrounded by agriculture or development. There are also areas that still contain large swaths of nearly continuous forest. This high variability in landscape structure makes Eastern Ontario an ideal location for this study. The size of the study region (~12000 km²) also allows for a large area from which to choose landscapes along gradients that allow us to test our predictions without correlation between landscape variables.

To identify study sites we first quantified values for three landscape variables—forest amount, forest fragmentation, and structural connectivity—within a radius of 1500 m around 1726, 30 m x 30 m forest interior sites across Eastern Ontario. From these candidate sites, we then selected 70 sites with low pairwise correlations among the three landscape variables. We surveyed these sites during the growing season (May-August) for forest understory plants and trees in 2020. Lastly, we tested our predictions using multiple regression models that measured the independent effects of each landscape variable on forest understory plant species richness, evenness, and site-level beta diversity. To determine the relevant spatial scale for estimating landscape context effects (the "scale of effect"; Jackson and Fahrig, 2015; Jackson and Fahrig, 2012), we fit models at 23 nested spatial scales from 500 to 6000 m.

Site selection:

Our objective for study site selection was to identify 70 forest interior sites. This was the maximum number we could survey for logistical reasons. For our forest cover data, we used a publicly available dataset (OMNRF, 2015) with sufficiently high resolution to delineate forest patches and forest corridors (i.e. hedgerows). This dataset defined patches as any treed area larger than 30 x 30 m, and hedgerows as linear treed areas that are 10-30 m wide. Forest was defined as any treed area with canopy cover >60% (OMNRF, 2015, Lee et al., 1998). This canopy cover was used for this dataset and our study because it is the minimum canopy cover requirement for forests using Ontario's ecological land classification system (Lee et al., 1998). We defined corridors as any treed area <30 m wide and >40 m long. The minimum corridor length corresponds to the minimum field edge length in our region. This size was used because it corresponds to the size of hedgerow corridors which occur in our study region, and the dimensions that would be the most practical to implement as a conservation action. A wooded corridor had continuous canopy cover with no gaps longer than 6 m. This gap size has previously been identified as large enough to significantly alter the connective function of corridors for seed dispersers (Bright, 1998; DEFRA, 2007).

We then edited this dataset to improve its accuracy, by hand-digitized the omitted treed areas using Google Earth satellite images of the region to detect the missing features (Google, n.d.). We digitized corridors and patches separately based on their dimensions. If the original dataset recorded an area as a corridor when it was wider than 30 m, we redigitized it as a patch. This process greatly improved the accuracy of the dataset, which improved our estimations of landscape variables (Figure 5).



Figure 5. Illustration of the difference between our dataset before and after hand-digitizing by comparing the original data set to Google Earth, shown for a small portion of the study region. The entire study region (see Figure 6) was edited in this process, which improved accuracy by adding corridors and small patches that were missed in the original dataset. Dark green polygons indicate the original dataset's treed patches, light green polygons indicate the original dataset's treed corridors, orange polygons indicate patches that were edited through digitizing, and light orange polygons indicate corridors that were edited through digitizing. Original dataset is the OMNRF's wooded areas dataset (2014).

Once we had mapped forest cover and delineated separate forest patches and corridors, we identified 1726 potential forest interior sample sites in our study area. These were in the southwest corner of each of the smallest 70% of forest patches in the study region. Very large patches were avoided to allow for variation in the number of patches and structural connectivity at high forest amount. We sampled only one site per patch to reduce spatial autocorrelation. The decision to sample the southwest corner was arbitrary, and the standardization was done to make in the field more efficient. The minimum patch size for sample sites was 200 m x 200 m to ensure that all sites were in the forest interiors (>50 m from the forest edge).

After identifying all 1726 potential sites, we calculated values for the three landscape variables within 500, 1000 and 1500 m of each potential site (Figure 6). These spatial scales were used for site selection because they correspond to relevant scales in previous studies of landscape-scale effects on plants (Vittoz and Engler, 2007, Lilley and Vellend, 2009; Vallet et al., 2010; Vinter et al., 2016; Oehri et al., 2020). Note, however, that during data analysis, we expanded the scales considered as suggested by Jackson and Fahrig (2015). Forest amount was calculated as the area of the landscape that was forested, i.e. covered by patches and corridors. Fragmentation was the number of forest patches in the landscape. Structural connectivity was the proportion of patches in the landscape that were both directly and indirectly connected via corridors (and patches) to the patch containing the survey site (Figure 7; Fall et al., 2007).

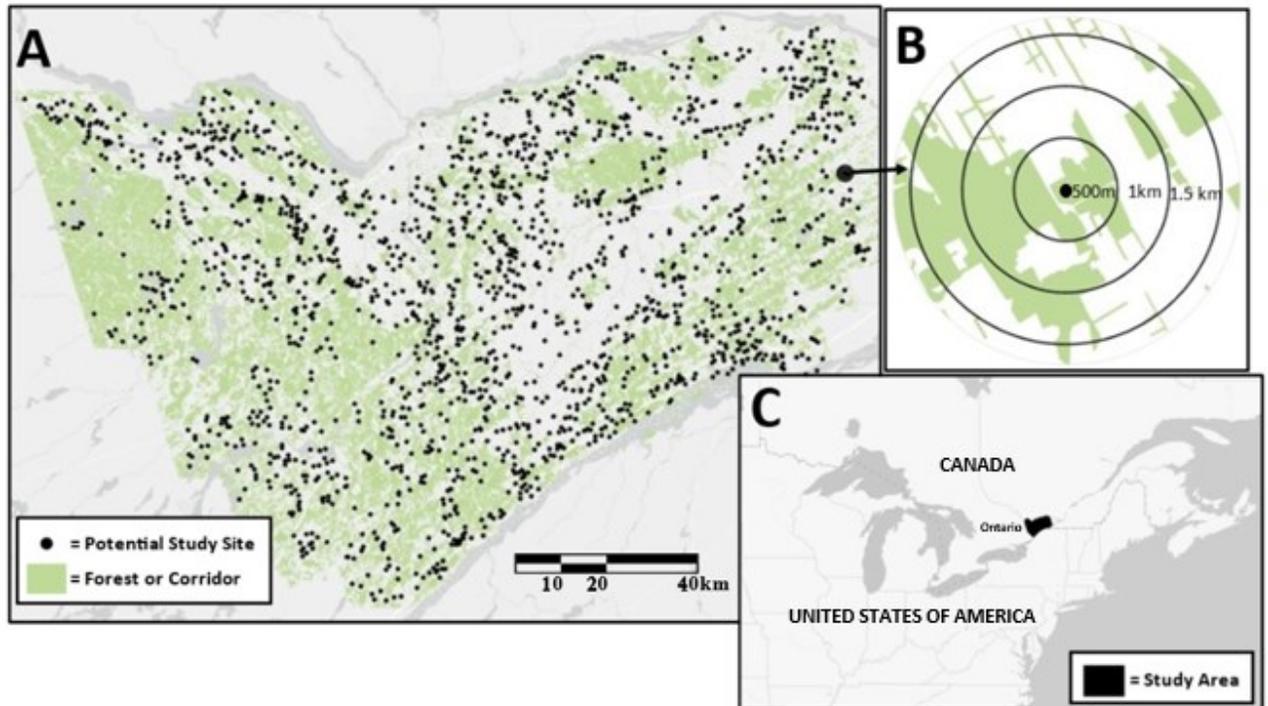


Figure 6. (A) Locations of all 1726 potential sample sites in the southwest corner of each forest patch in eastern Ontario, excluding very large patches. Potential sites were in forest interior. (B) Example of the spatial extents within which we measured forest amount, forest fragmentation (number of patches), and structural connectivity (proportion of patches in the landscape connected to the patch containing the potential sample site) in the landscape surrounding each potential site. The landscape variables were measured within 500m, 1000m, and 1500m of potential sites during the site selection process. (C) The location of the study area in eastern Ontario, Canada.

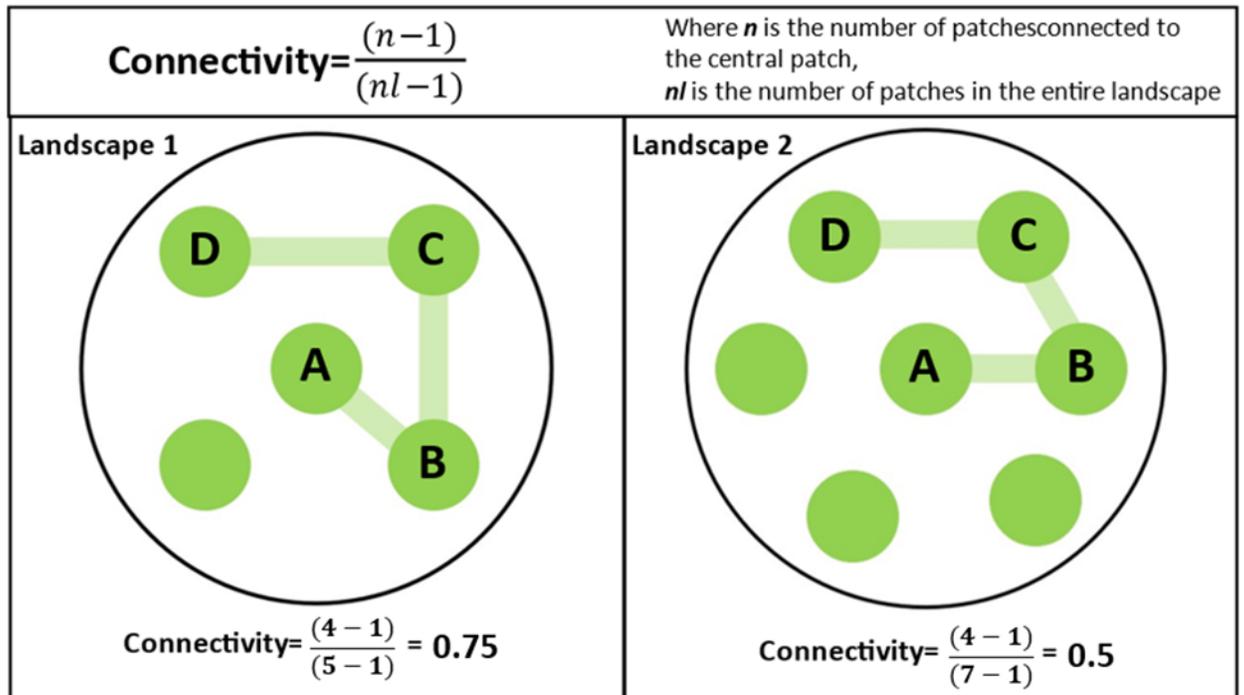


Figure 7. Illustration of structural connectivity calculation, where dark green circles represent forest patches, and light green lines represent corridors. Structural connectivity was the proportion of patches in the landscape that are connected to the patch containing the survey site (excluding that patch itself), either directly or indirectly. Therefore, connectivity is relative to the maximum possible connectivity, given the number of patches present. Landscapes 1 and 2 have the same number of patches connected to the central patch, but landscape 1 has higher structural connectivity because there are fewer patches in the landscape.

After estimating the landscape predictor variables for all potential sample sites, we selected 300 candidate sample sites where landowners were contacted for permission to complete the surveys. These sites were selected to minimize the correlation between landscape variables and maximize the range of landscape variable values at all three spatial extents. Our other criteria for site selection were as follows. First, we aimed to intersperse the site types (i.e. high or low habitat amount, fragmentation, and connectivity values) across the study region to avoid confounding predictor variables with unmeasured variables such as regional gradients in disturbance or soil type. Second, sites were located

>3 km from one another to avoid spatial autocorrelation. Finally, we minimized site-scale variation in forest type by only selecting sites that were classified as deciduous or mixed forests (Environment Canada, Unpublished). From these 300 initially selected candidate sites, we gained permission for and surveyed 70 sites.

Plant surveys:

The 70 sites were surveyed in an order that mixed sites with low and high values of each landscape variable, to avoid any correlation between date of survey and the landscape variables. Every 4 days, 8 sites were surveyed, representing all combinations of low/high values for each of forest amount, fragmentation, and structural connectivity. Each site was visited twice, for a total of 140 plant surveys during summer 2020. All surveys were conducted by the first author between May 11th and August 23rd. At each site, we surveyed a 184 m² area for plant understory species and a 120 m² area for tree species (Figure 8). Understory plants were the species of interest in our analyses; the tree surveys were used to control for variation in local site conditions (see below). Plant surveys were completed in two visits: a first visit in May or June, and a second in July or August. Figure 8 shows the orientation and placement of quadrats and transects in each site. During each visit, the cover and identity of understory plant species (< 1 m height) were recorded in 8 6.5 m² quadrats. After the quadrats were surveyed, a 40 m² understory belt transect was surveyed, where any plant species not already observed in the quadrats were recorded. Lastly, a 120 m² tree belt transect was surveyed on the second visit where the species and abundance of trees >5 m tall were recorded for a wetness index. Also on the second visit, canopy cover over the area surveyed for understory plants was visually

assessed as being greater than or less than 60% canopy cover. The 60% threshold for canopy cover is used to distinguish between forests (>60%) and woodlands (<60%), which are considered different ecosites in Eastern Ontario (Lee et al., 1998). Each site visit took between 3-5 hours to complete.

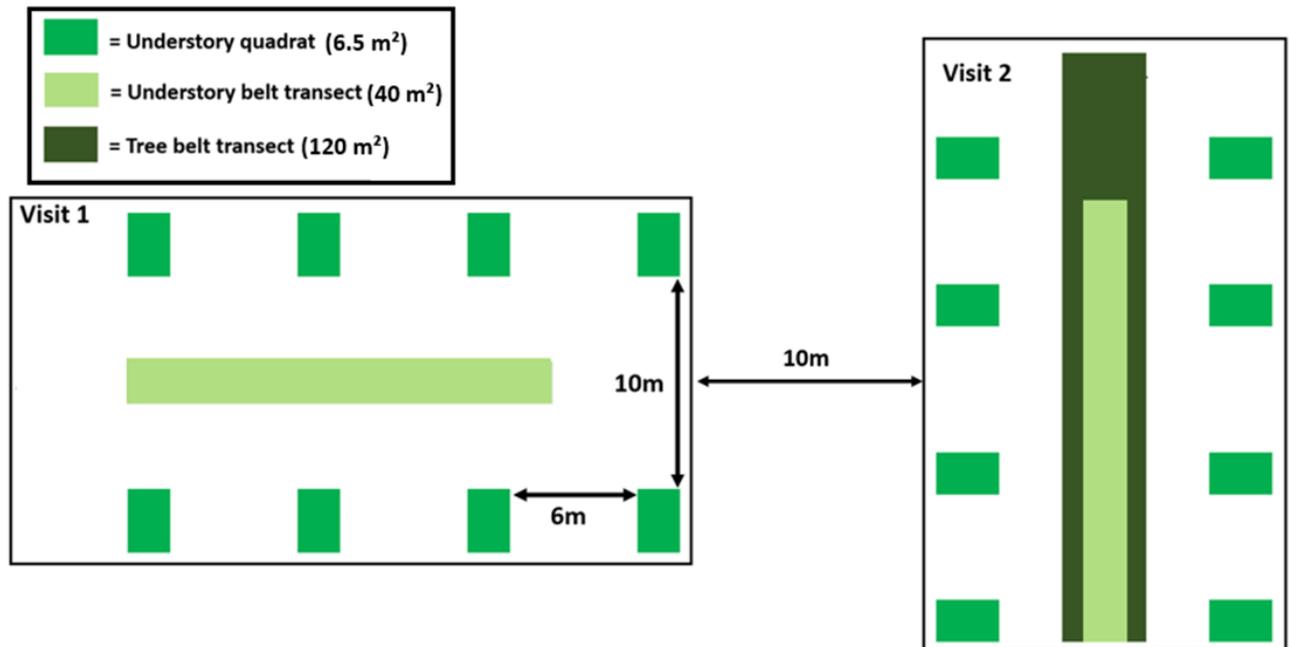


Figure 8. Layout of the quadrats and belt transects used to survey plants in 70 interior forest sites. Surveys were completed in two visits, where 8 understory quadrats and an understory belt transect were surveyed at each site in each visit. In quadrats, the cover-abundance class and identity of each species were recorded. In understory belt transects, the identity of species that were not already observed in quadrats were recorded. In addition, on the second visit, a tree belt transect was surveyed for tree species presence and abundance.

All plant species were identified by the first author using taxonomic distinctions in the Michigan Flora (Voss and Reznicek, 2012), which is a commonly used flora for Eastern Ontario. In most cases (92.2%), plants were identified to the species level. If this was not possible due to key identifying features being absent, identification was made to

genus or family level. These genus and family level classifications were treated as species in our analysis. In most cases, identification was done in the field. When this was not possible, plants were identified later from notes and photos taken in the field.

Cover-abundance measurements for each species in each quadrat were made using the extended Braun-Blanquet cover-abundance scale (Table 1; van der Maarel, 2007). This approach is more efficient than using detailed cover measurements (e.g. to the nearest %), and it performs well in statistical analyses (Damgaard, 2014). We transformed the data to convert classes to mean cover values as in van der Maarel (2007) (Table 1).

Table 1. Ranges of cover and abundance used to place each species in each quadrat into one of 9 cover-abundance classes. See van der Maarel, 2007.

Cover-Abundance Class	Cover Range	Abundance Range	Transformed Cover
r	0-5%	1	0.5
+	0-5%	2-6	1
1	0-5%	6-50	2
2m	0-5%	50+	4
2a	5-12.5		8.75
2b	12.5-25		18.75
3	25-50		37.5
4	50-75		62.5
5	75-100		87.5

Data analysis:

To test our predictions, we estimated values for five understory plant response variables at each site: species richness, proportion of species that are forest interior specialists, proportion of species that were non-native species, species evenness, and site contribution to beta diversity. Landscape variables were estimated at multiple spatial extents around each survey site, from 500 to 6000 m radius, in 250 m increments. We also calculated two potentially confounding site level variables that might obscure effects

of landscape variables: a wetness index based on the tree surveys (see below), and canopy cover. Lastly, we tested each of our 11 predictions, building statistical models at multiple spatial extents to determine the scale of effect of landscape variables on the response.

Response variables:

Species richness (predictions 1-4) was the number of understory plant species that were found at each site from both visits combined. For the proportion of species at each site that were forest interior specialists (prediction 5), classifications into forest specialists and generalists were based on their habitat description in Haines, Farnsworth, and Morrison (2011) and Voss and Reznicek (2012). If a species was described by these authors as only occurring in a forest or treed swamp interior (not including edges), it was categorized as a forest interior specialist. If a species was described as occurring in any other environment, it was considered a non-specialist. For the proportion of species at each site that were non-native (prediction 6) we used regional plant species lists that include information on native status in Ontario (NHIC, 2021). For the proportion of plant species that were short distance dispersers (prediction 7), we categorized species as short or long-distance dispersers based on their dispersal morphology. Species that have adaptations for dispersal by animals (via ingestion or attachment) or wind were assumed to be capable of long-distance dispersal, and species dispersed by water, explosions, ants, or that lack any specific dispersal adaptation were assumed to be short distance dispersers (Vitoz and Engler, 2007).

Plant species evenness (prediction 8) was calculated at each site using “Pielou’s J ” (Pielou, 1966; Equation 1), which measured the extent to which abundances were equally distributed across plant species. Higher evenness values represent more similar abundances among species at a site.

Equation 1.

$$J = \frac{\sum_{i=1}^S p_i \times \ln(p_i)}{\ln(S)},$$

where p_i was the mean proportional quadrat cover of species i at the site (cover across all 16 quadrats), and cover was estimated as the transformed Braun-Blanquet cover-class value (Van der Maarl, 2007; Table 1). S was the number of species found in all 16 quadrats at a site. This commonly used evenness metric was chosen because it is simple to calculate and has proven to be an unbiased measure of species evenness (Jost, 2010).

Finally, each site’s contribution to the dataset’s overall beta diversity (prediction 9) was measured by calculating the “Local Contribution to Beta Diversity” metric (Legendre and De Cáceres, 2013). This measure determines the uniqueness of a site’s community composition when compared to all sites in the sample. See Legendre and De Cáceres (2013) for more details and diagrammatic representation of the calculation. This variable was calculated using the “adespatial” package in R.

Landscape predictor variables:

Landscape predictor variables were estimated at multiple nested spatial extents (500-6000 m radius in 250 m increments) to identify the scale of effect of landscape

variables on the response. Forest amount, fragmentation, and structural connectivity were calculated in the same way as during the site selection process (see above). Forest interior amount was forest amount excluding the outer 30 m of patches and corridors. An edge distance of 30 m was used because past studies have found this is the maximum distance to which forest edges influence plant species in temperate forests (Fraver 1994; Honnay et al. 2002).

Potential confounding variables:

In addition to the landscape variables, we included two site scale variables that might affect understory plant diversity: wetness and canopy cover (Cornwell and Grubb, 2003; Zarfos et al., 2019; Pausas and Austin, 2001). The wetness index was calculated using wetness coefficients and abundances of the trees at the site (NHIC, 2021; Equation 2). Wetness coefficients represent the level of moisture in which a plant species can survive and range from -5 to 5, where -5 denotes an obligate wetland species, and +5 denotes an obligate upland species (Oldham, Bakowsky and Sutherland, 1995). The canopy cover was binary and split sites into two categories: >60% coverage and ≤60% coverage.

Equation 2.

$$\text{Wetness Index} = \sum_{i=1}^S (\text{Coefficient of Wetness}_i \times p_i),$$

where p_i was the proportion of all trees in the belt transect (Figure 8) that were species i .

Statistical models:

We used generalized linear modelling to test our predictions. Models are summarized in Table 2. All models also contained the two site-scale variables (wetness and canopy cover).

Table 2. The combination of model type, response variables, and landscape variables used to test each prediction. Each model also contained two site scale predictor variables (canopy cover and wetness index) to control for effects of local site conditions.

Prediction	Model type	Response Variable	Landscape Scale Predictor Variables
1-3 (+, -)	Negative Binomial Generalized Linear Model	Species Richness	Forest amount, Number of patches, Structural connectivity
4	Negative Binomial Generalized Linear Model	Species Richness	Interior amount, Number of patches, Structural connectivity
5	Beta Regression Model	Proportional Species Richness of Forest Interior Specialists	Interior amount, Number of patches, Structural connectivity
6	Beta Regression Model	Proportional Species Richness of Non-Native Species	Interior amount, Number of patches, Structural connectivity
7	Beta Regression Model	Proportional Species Richness of Short-Distance Dispersers	Interior amount, Number of patches, Structural connectivity
8	General Linear Model	Evenness	Forest amount, Number of patches, and Structural connectivity

All models were estimated using the landscape variables calculated at multiple nested scales to empirically determine the scale of effect of the landscape context on each response. Lack of variability in structural connectivity at scales below 750 m and above 2500 m precluded including structural connectivity in models at those scales (Appendix figure boxplots). Therefore, models including structural connectivity were conducted only from 750 to 2500 m scales. We also ran models excluding structural connectivity at scales from 500 to 750 m and from 2500 m to 6000 m. We selected the model at the scale where the delta AIC was lowest, as suggested by Jackson & Fahrig (2014).

Results

Site and landscape characteristics:

Low and high values of the landscape predictors were widely distributed over the region (Figure 9). Note that the low and high categories were used only for site selection; in data analyses, the predictor variables were modelled as continuous variables. Pairwise spearman rank correlations among the three landscape variables across the 70 sample sites at the scales of effect identified in the modelling process ranged from absolute values of 0.0007 to 0.286 (Figure 10). In our original the subset of 1726 potential study sites, the correlation between forest amount and fragmentation was already low (0.186). This low correlation was achieved by selecting sites in the southwest corner of the smallest 70% of forest patches in the study region. Prior to selecting this subset of sites- when considering all points in forest patches >50 m from the edge and 30 m from each other- correlation between forest amount and fragmentation was high (0.619) (Figure 11). Spearman rank correlations were used in this analysis because the relationship between forest amount and fragmentation is known to be nonlinear across the entire range of values (Püttker et al, 2020).

Interior habitat amount was highly correlated with total forest amount (0.984) but had low correlations with fragmentation and structural connectivity (spearman rank correlations between 0.126 and 0.286). Wetness index ranged from -3 to 3 across sites, with a mean of 1.1. Three sites had canopy cover under 60%, and 67 sites had canopy cover over 60%.

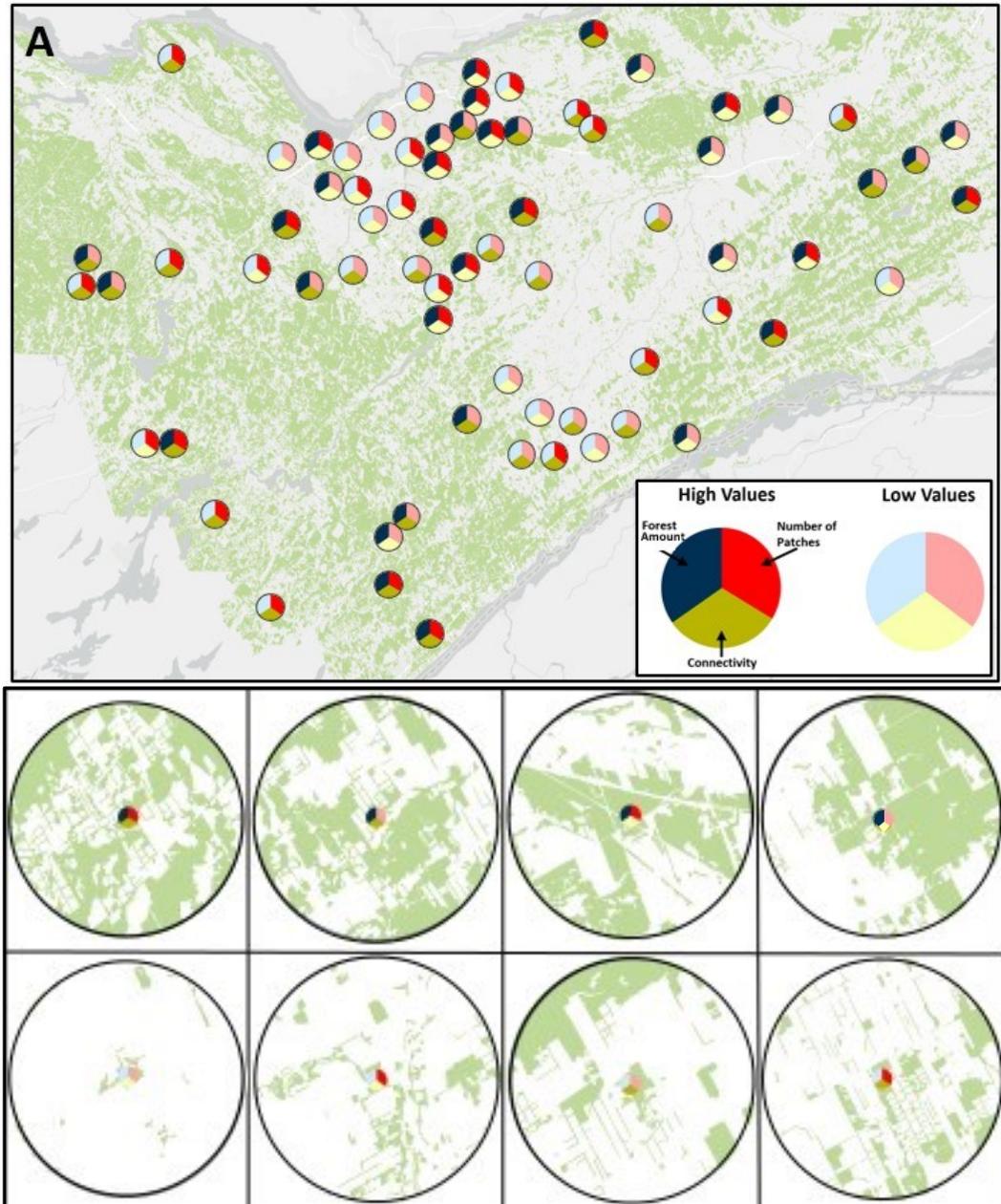


Figure 9. **A.** Locations of the 70 interior forest sites where understory plants were surveyed. For visual presentation, each of the three landscape predictors are classed as low (lower 50%) or high (upper 50%) within 1500m of the sample sites. Analyses were conducted using continuous values of the landscape predictors, at multiple spatial scales. Green is forest cover. **B.** Example landscapes. Green polygons are forested landcover (patches and corridors), and black circles show extent of the 1500m-radius landscape surrounding the sample sites. The plant sample sites are shown as colored circles at the center of each landscape. The low and high categories were used only for site selection; in data analyses the predictor variables were modelled as continuous variables.

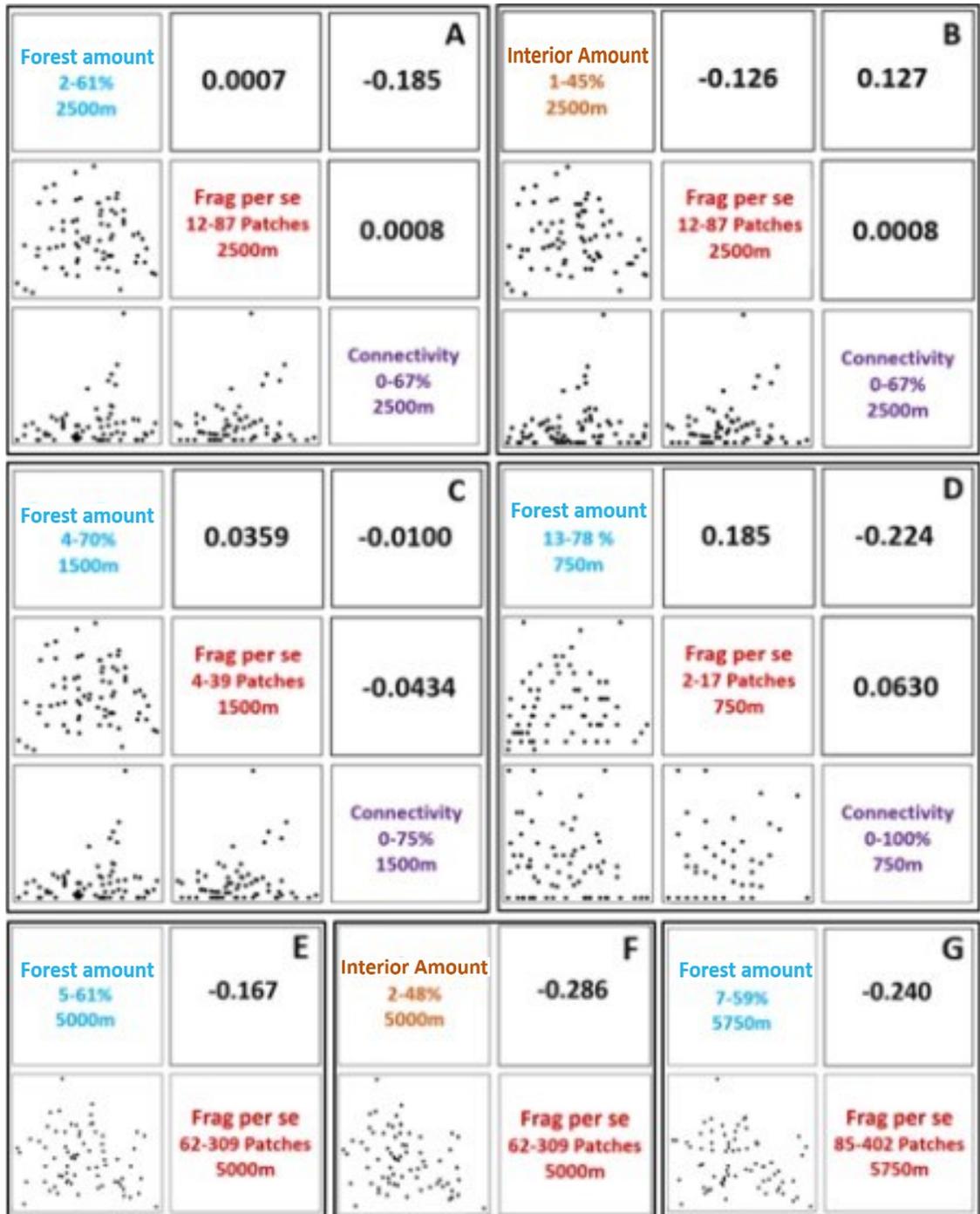


Figure 10. Scatterplots and pairwise spearman ranked correlations for predictor variables at the scales of maximum effect for each prediction test: 1-5 (A and E), 6 (B and F), 9 (C and E), and 10 (D and G). The scale of maximum effect is the scale at which the landscape variables produce the model with the lowest delta AIC. Each individual point represents the landscape variable values for one site at the scale of maximum effect.

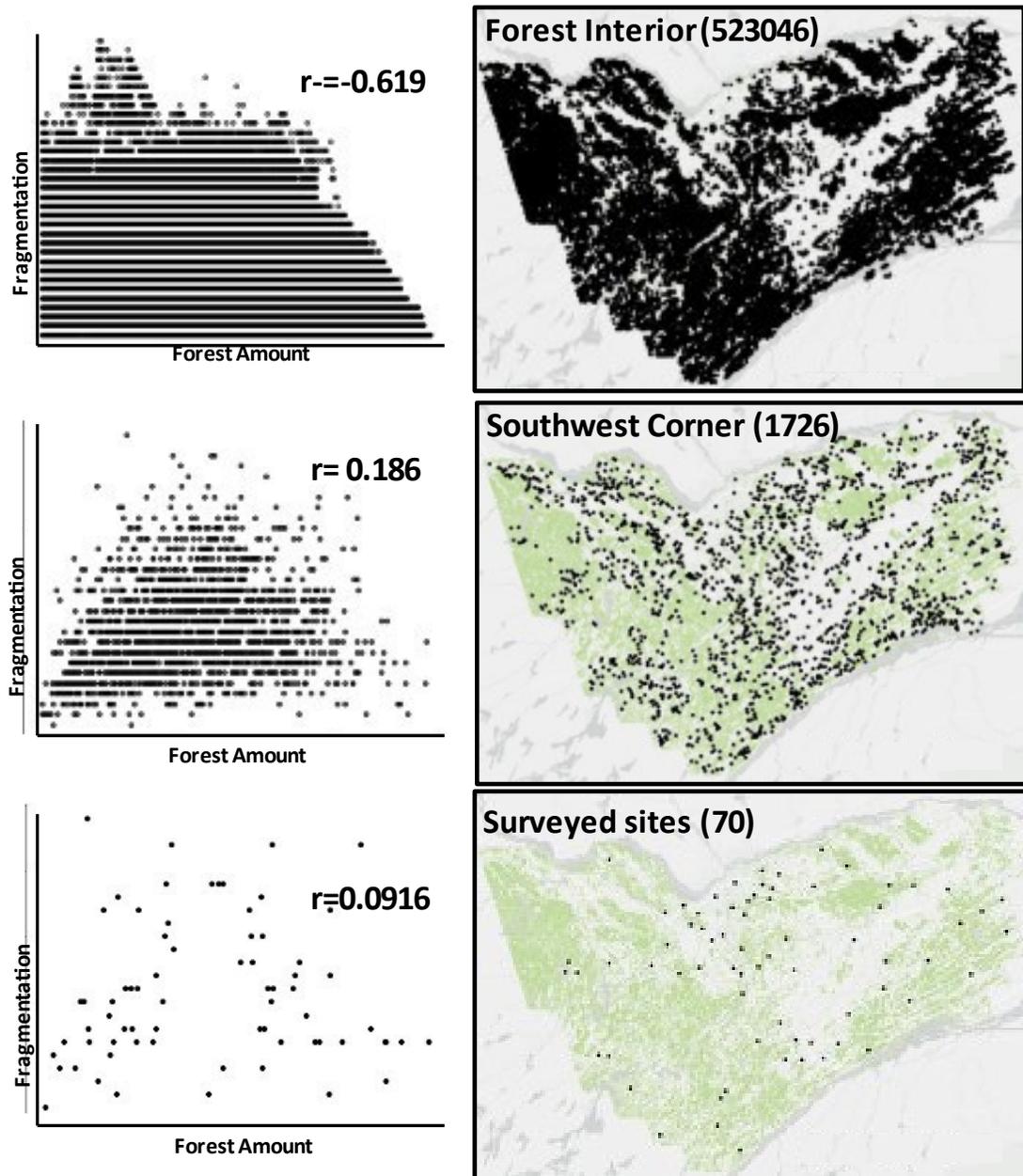


Figure 11. Correlation between forest amount and fragmentation at different stages of the site selection process. The top graph/map shows all considered sample sites >50 m from the forest edge and 30 m from each other (n=523046). The middle graph depicts the subset where only the southwest corner of the 70 smallest patches was considered (n=1726). The lower graph/map depicts the chosen sample sites that were surveyed and used to produce results (n=70). Spearman rank correlations are shown beside each graph, with correlation being the highest prior to choosing a subset of sites, and correlation decreasing as site selection progressed.

Plant response data:

In all, we recorded 251 different understory plant taxa. Of these, 239 were identified to species, 10 were identified to genus, and 1 was identified to family (Poaceae spp). The median species richness per site was 41 species, with 16 to 72 species per site. Cover of species varied greatly across species, with a few common species accounting for a large portion of the total cover across all sites (Figure 12). The most common species observed were *Carex spp* (Sedge Species), *Acer saccharum* (Sugar Maple), *Maianthemum canadense* (Canada mayflower), *Onoclea sensibilis* (Sensitive fern), and *Frangula alnus* (Glossy buckthorn), which made up 6.75%, 6.47%, 5.27%, 4.16%, and 3.4% of total species cover respectively. Forest interior specialists made up 31% of the species identified in the study, with a median value of 32% of species per site (proportions ranged from 6 to 65%) (Table Supplementary species list). Non-Native species made up 10% of all species identified in the study, with a median value of 7.2% of species per site (proportions ranged from 0 to 35%). Species evenness varied from 0.30 to 0.83 across sites, with a median value of 0.75. Local contribution to beta diversity ranged from 0.0096 to 0.022 across sites, with a median value of 0.014.

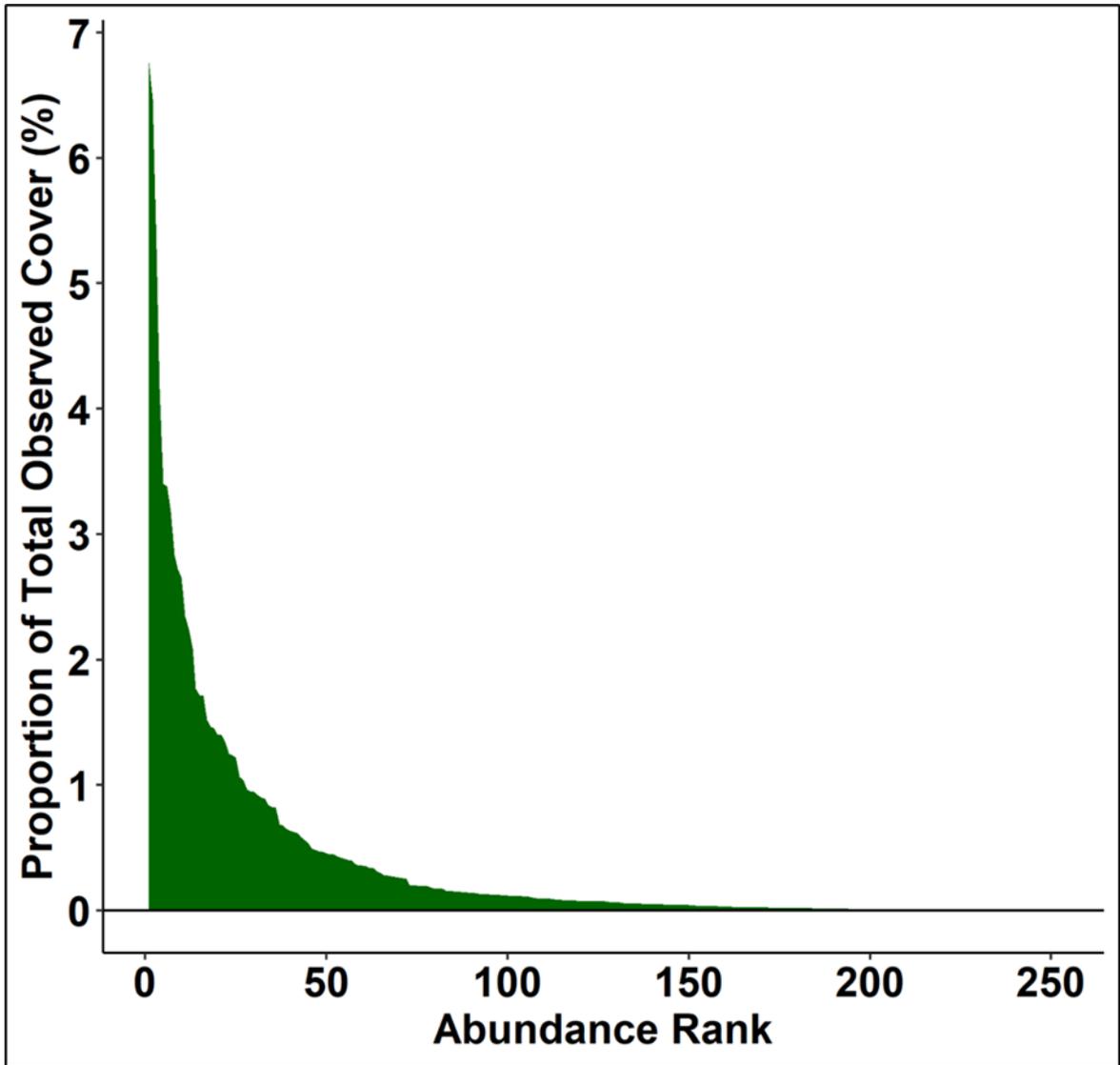


Figure 12. Rank-abundance plot showing the proportion of species cover across all sites belonging to each species by rank. Species are arranged in order from most to least abundant in terms of cover.

Prediction 1:

Our results supported the prediction that understory plant species richness at a site increases with forest amount in the surrounding landscape (the 95% confidence interval for the effect is greater than zero). This effect was stronger than the effects of fragmentation and structural connectivity (Figure 13). The effect of forest amount was positive across scales, with the strongest relationship at 4750 m.

Predictions 2+ and 2-:

Our results support prediction 2+ rather than prediction 2-. Plant species richness decreased with forest fragmentation (Figure 13). This effect was present at larger spatial scales, and was strongest at 5000 m.

Predictions 3+ and 3-:

Neither of our predictions for the relationship between connectivity and understory plant species richness was supported, as species richness at sample sites was not strongly related to structural connectivity at any spatial extent (Figure 13).

Prediction 4:

Our results supported the prediction that interior forest amount is a better predictor of species richness than total forest amount. However, the difference between the two models was small (Figure 14), likely due to the extremely high correlation between interior forest amount and total forest amount ($r = 0.984$).

The effect of forest fragmentation remained negative but was weaker in the model containing interior forest amount than the model containing total forest amount (Figure 14). Connectivity results remained weak.

Prediction 5:

Our results did not strongly support the prediction that sites surrounded by landscapes with more fragmentation and with higher connectivity contain a lower proportion of forest interior specialists (Figure 15).

Prediction 6:

There was weak support for the prediction that sites surrounded by landscapes with more interior forest would have a lower proportion of non-native species (Figure 16). Effects of fragmentation and connectivity on the proportion of non-native species were weak (Figure 16).

Prediction 7:

Our results supported the prediction that sites surrounded by landscapes with more fragmentation would contain a lower proportion of short distance dispersers (Figure 17). Our results did not support the prediction that the proportion of short distance dispersers would increase with more structural connectivity.

Prediction 8:

Our results supported the prediction that species evenness declines with increasing fragmentation and structural connectivity (Figure 18). The fragmentation effect was consistently negative and strongest within 5000 m of sample sites. The structural connectivity effect was also negative and strongest at 1250 m. However, this relationship was strongly influenced by a single site with the highest structural connectivity. Our results only weakly supported our prediction that species evenness would decline with increasing forest amount.

Prediction 9:

Our results supported the predictions that a site's contribution to beta diversity declines with forest amount and structural connectivity (Figures 19). Sites had a lower contribution to beta diversity when the patch containing the site was more connected to other patches in the landscape, especially at the smallest spatial scale (750 m). Sites had a higher contribution to beta diversity when surrounded by less forest measured at larger spatial scales (4500-6000 m scales). Our results did not support our prediction that a site's contribution to beta diversity decreases with increasing forest fragmentation.

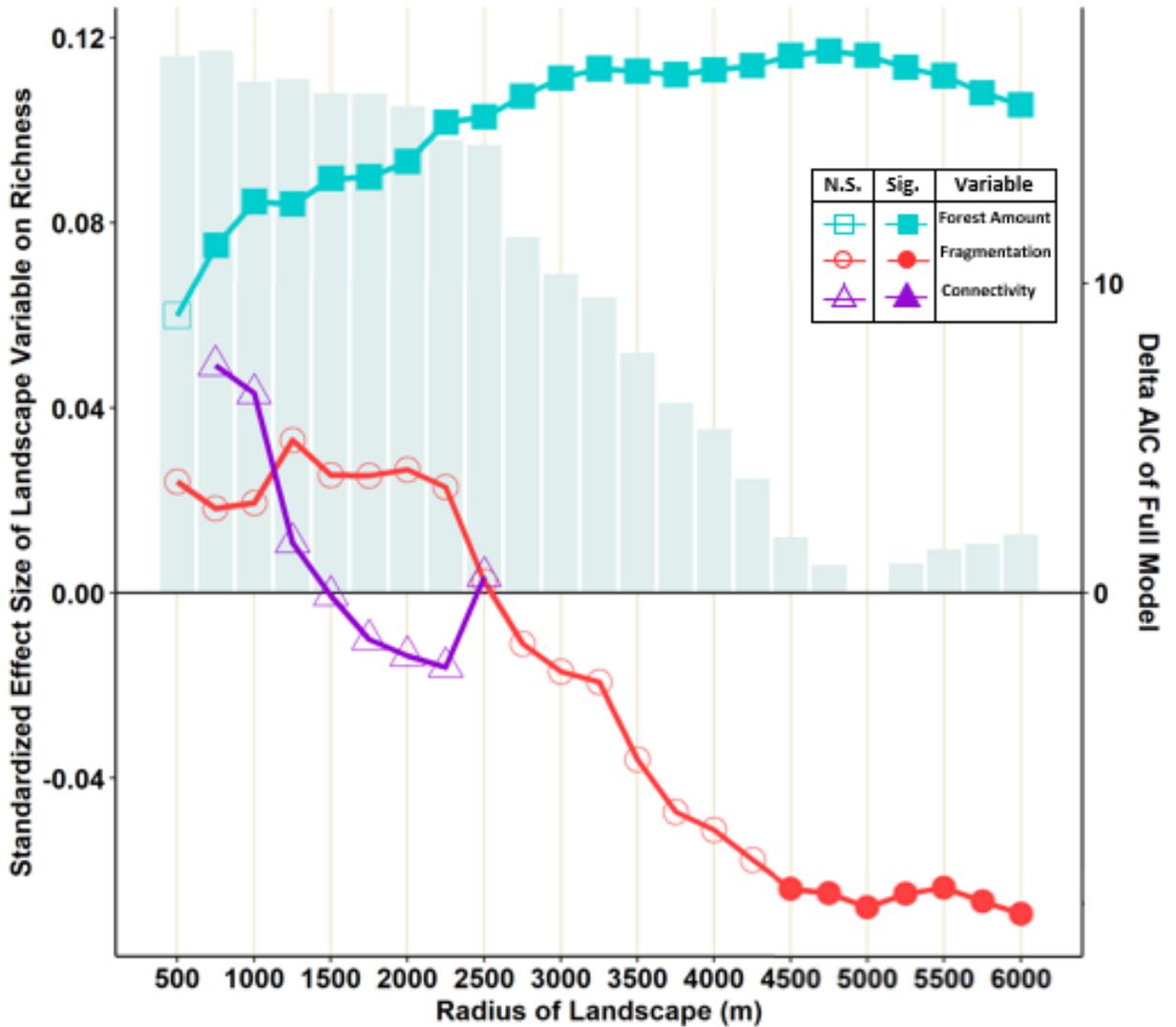


Figure 13. Standardized coefficients from models of the effects of surrounding forest amount, forest fragmentation (number of forest patches), and structural connectivity on species richness of understory plants survey in 70 forest sites. All three landscape variables were included at the 750-2500m scale. Forest amount and fragmentation were included at the 500m and 2750m-6000m scales. The Delta AIC for the model at each scale is shown as grey bars, where the scale without a bar indicates the model with the best fit. Solid symbols represent effects where the confidence interval was $\leq 95\%$ the effect size.

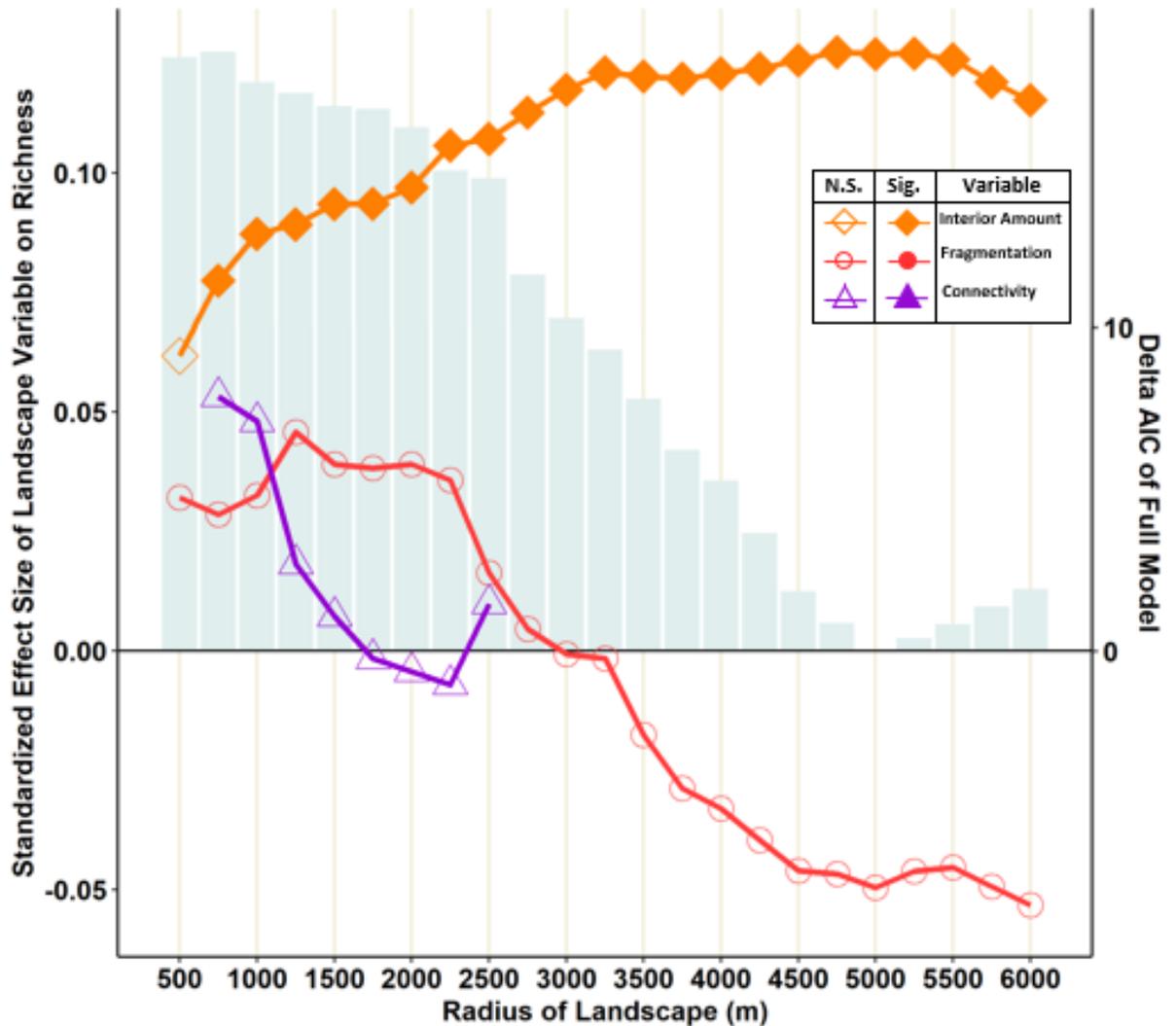


Figure 14. Standardized coefficients from models of the effects of surrounding interior amount (forest amount not including edges), fragmentation (number of forest patches), and structural connectivity on species richness of understory plants survey in 70 forest sites. All three landscape variables were included at the 750-2500m scale. Forest amount and fragmentation were included at the 500m and 2750m-6000m scales. The Delta AIC for the model at each scale is shown as grey bars, where the scale without a bar indicates the model with the best fit. Solid symbols represent effects where the confidence interval was $\leq 95\%$ the effect size

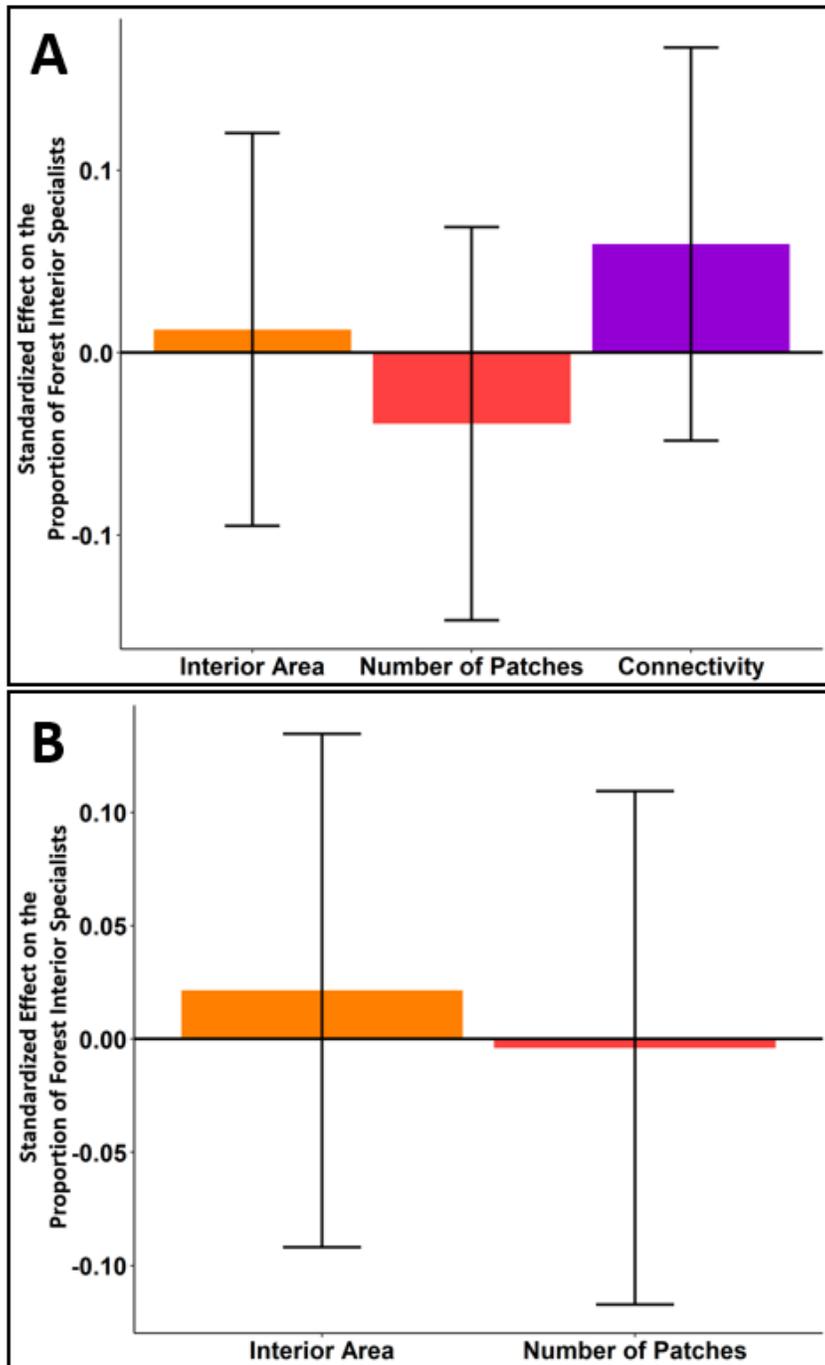


Figure 15. Relationships between the proportion of species that are forest interior specialists at forest sites and interior habitat amount, fragmentation (number of patches), and structural connectivity in the landscapes surrounding the sites. Interior amount is the amount of forest habitat in the surrounding landscape not including the outer 30m of habitat patches. (A) is the output from the model with all three landscape variables at 2500m and (B) is the output from the model with interior amount and number of patches at 5000m. Error bars show 95% confidence intervals.

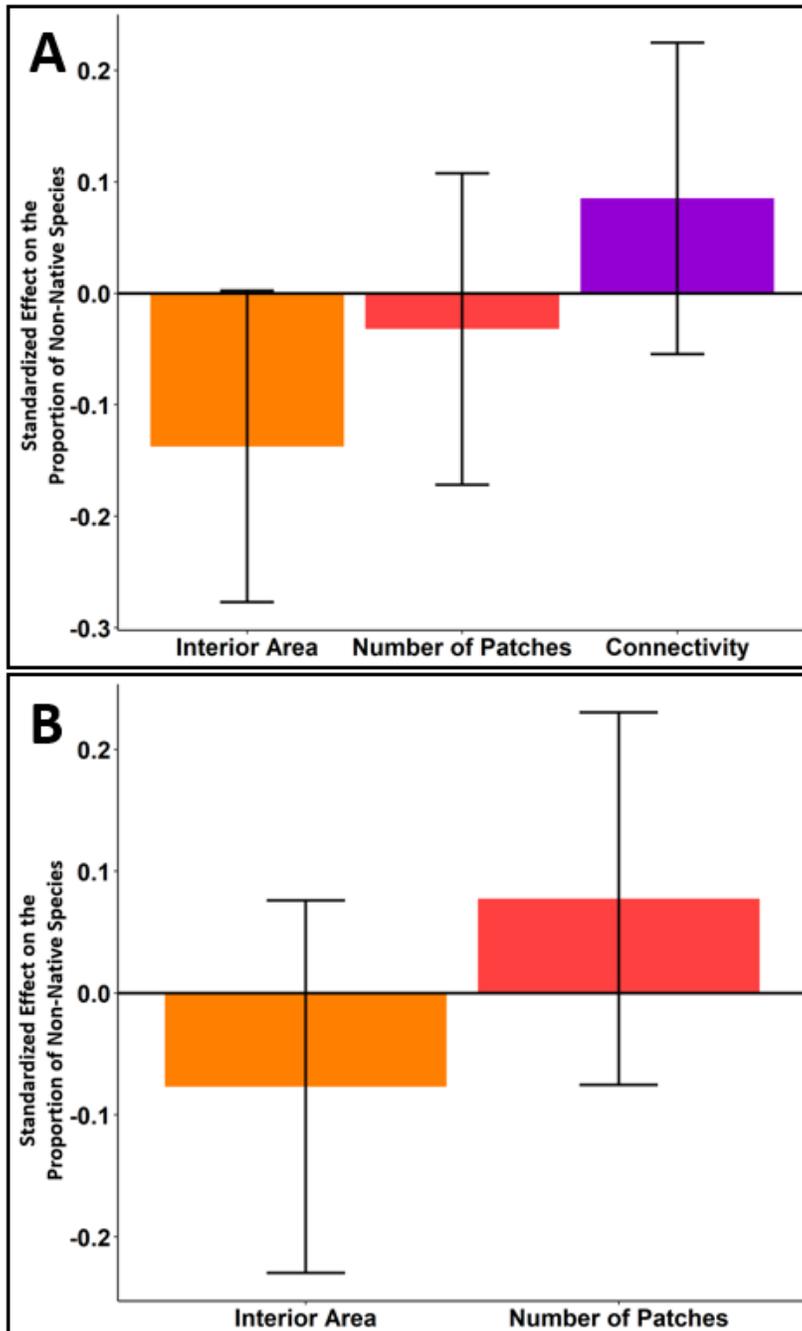


Figure 16. Results from proportional richness models that tested the relationship between the proportion of species that are non-native at a forest site and interior amount, fragmentation (as number of patches), and connectivity. The interior amount variable was used in these models, which is the amount of forest habitat in a landscape unit when not including the forest edge (outer 30m of habitat patches). Orange represents interior amount, red represents fragmentation, and purple represents connectivity. A) is the output from the trivariate model with all variables at 2500m, and (B) is the output from the bivariate model with all variables at 5000m. Each bar represents the standardized effect size of a variable. Error bars show 95% confidence intervals.

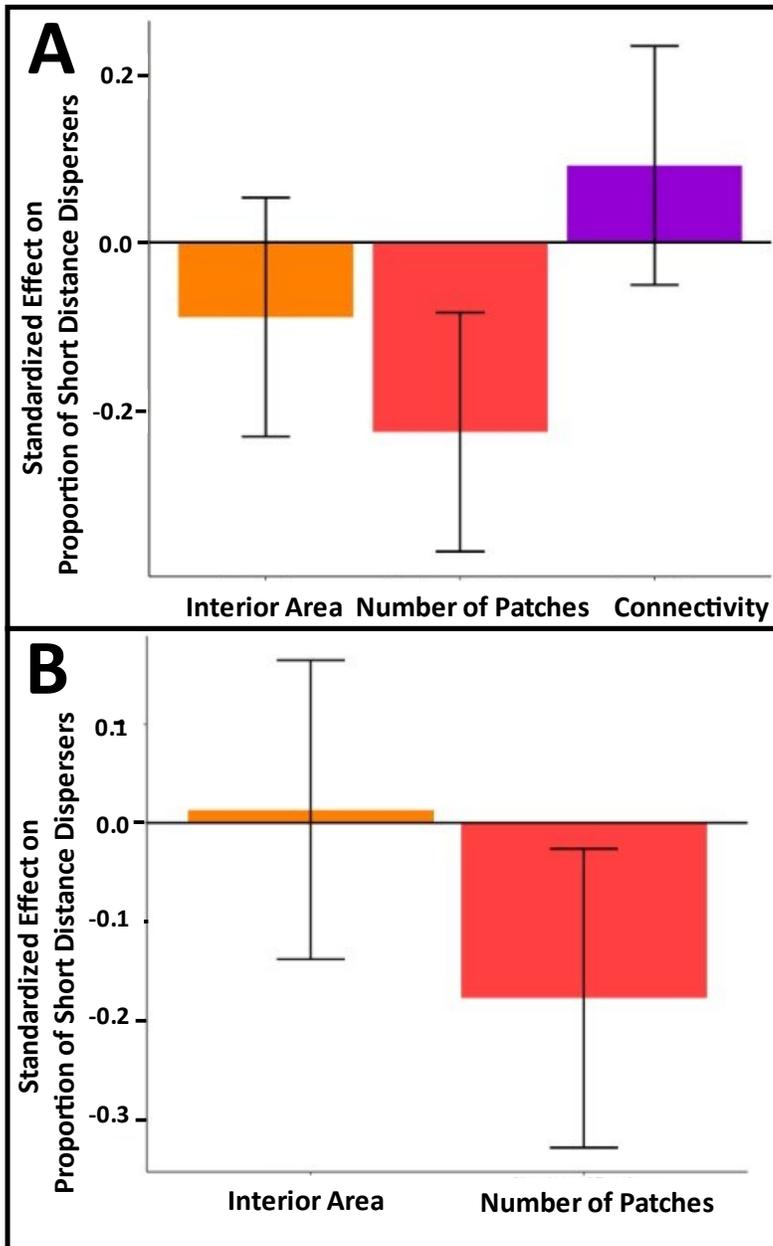


Figure 17. Results from proportional richness models that tested the relationship between the proportion of species that are short distance dispersers at a forest site and interior amount, fragmentation (as number of patches), and connectivity. The interior amount variable was used in these models, which is the amount of forest habitat in a landscape unit when not including the forest edge (outer 30m of habitat patches). Orange represents interior amount, red represents fragmentation, and purple represents connectivity. A) is the output from the trivariate model with all variables at 2500m, and (B) is the output from the bivariate model with all variables at 5000m. Each bar represents the standardized effect size of a variable. Error bars show 95% confidence intervals.

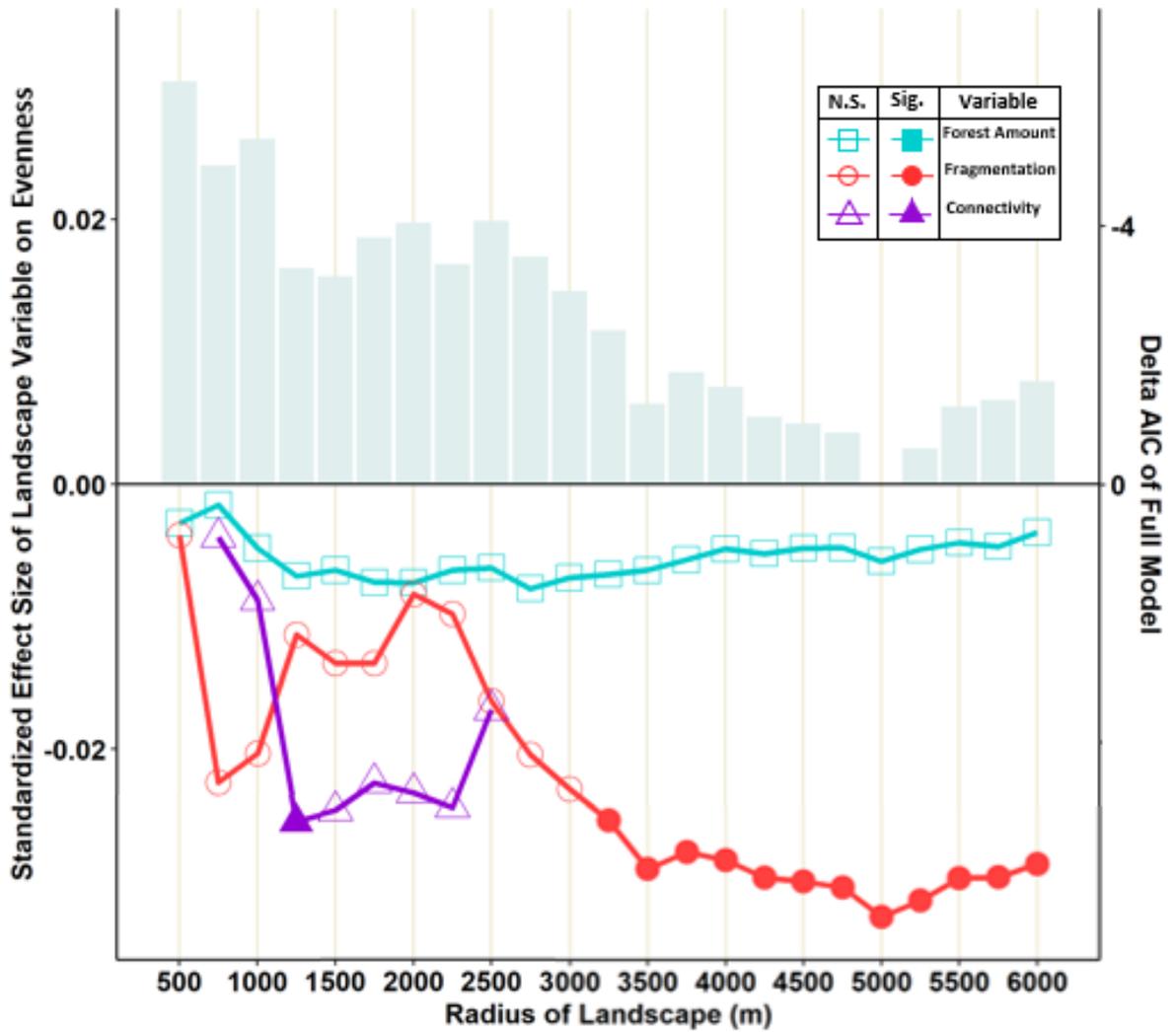


Figure 18. Standardized Coefficients from models of the effects of surrounding forest amount, fragmentation (number of forest patches), and connectivity on species evenness of understory plants survey in 70 forest sites. All three landscape variables were included at the 750-2500m scale. Forest amount and fragmentation were included at the 500m and 2750m-6000m scales. The Delta AIC for the model at each scale is shown as grey bars, where the scale without a bar indicates the model with the best fit. Solid symbols represent effects where the confidence interval was $\leq 95\%$ the effect size.

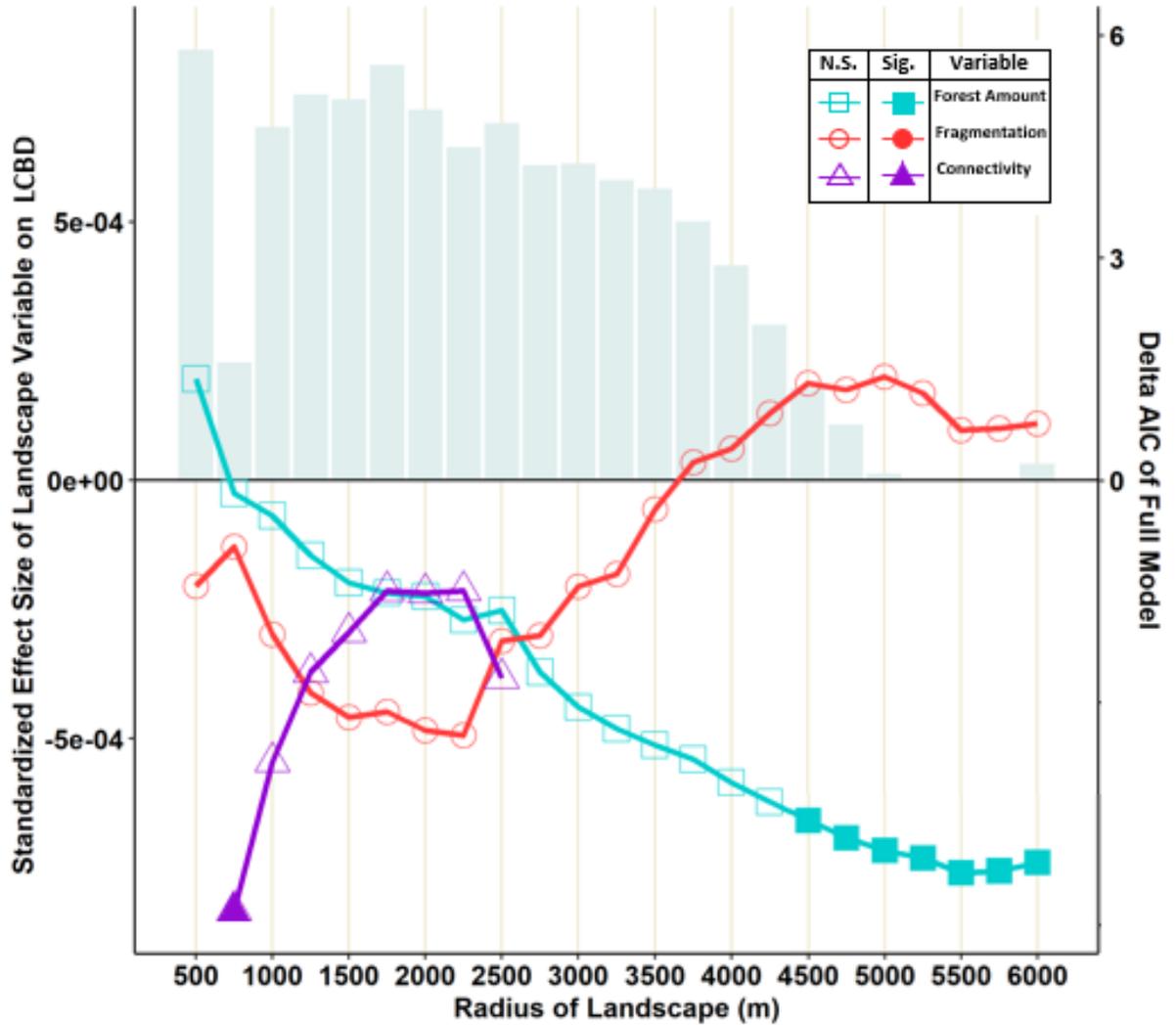


Figure 19. Standardized Coefficients from models of the effects of surrounding forest amount, fragmentation (number of forest patches), and connectivity on local contribution to beta diversity of understory plants survey in 70 forest sites. All three landscape variables were included at the 750-2500m scale. Forest amount and fragmentation were included at the 500m and 2750m-6000m scales. The Delta AIC for the model at each scale is shown as grey bars, where the scale without a bar indicates the model with the best fit. Solid symbols represent effects where the confidence interval was $\leq 95\%$ the effect size.

Discussion

Effects of forest amount

As expected, habitat amount had strong positive effects on species richness. Past studies have explored this effect in detail and have consistently found that increasing habitat area in the landscape increases site-scale species richness (Fahrig, 2013; Benchimol et al., 2017).

Furthermore, we found that although sites in landscapes with low habitat amount had fewer species, their species were more unique in relation to the species across the 70 sites. In other words, a site's contribution to beta diversity decreased with increasing habitat amount in the surrounding landscape. We speculate that this effect is due to greater isolation of sites in landscapes containing less forest, causing a greater role of ecological drift relative to competition (Macdonald et al, 2018; Vellend, 2010; Hubbell, 2005). With this increasing role of ecological drift, competitively dominant species that tend to be common in a high-habitat landscape are more likely to decrease in dominance due to random factors, leaving room for less competitive uncommon species to persist (Vellend, 2010) (Figure 20). Habitat isolation should also decrease recolonization rates (Brown and Kodric-Brown, 1977), making sites in landscapes with less forest more favorable for the persistence of uncommon species that were present at the site before habitat loss (Deane and He, 2018). This argument is consistent with the findings of patch-scale studies, which find that small, isolated patches have more rare and uncommon species than larger patches (Deane and He, 2018; Wintle et al., 2019).

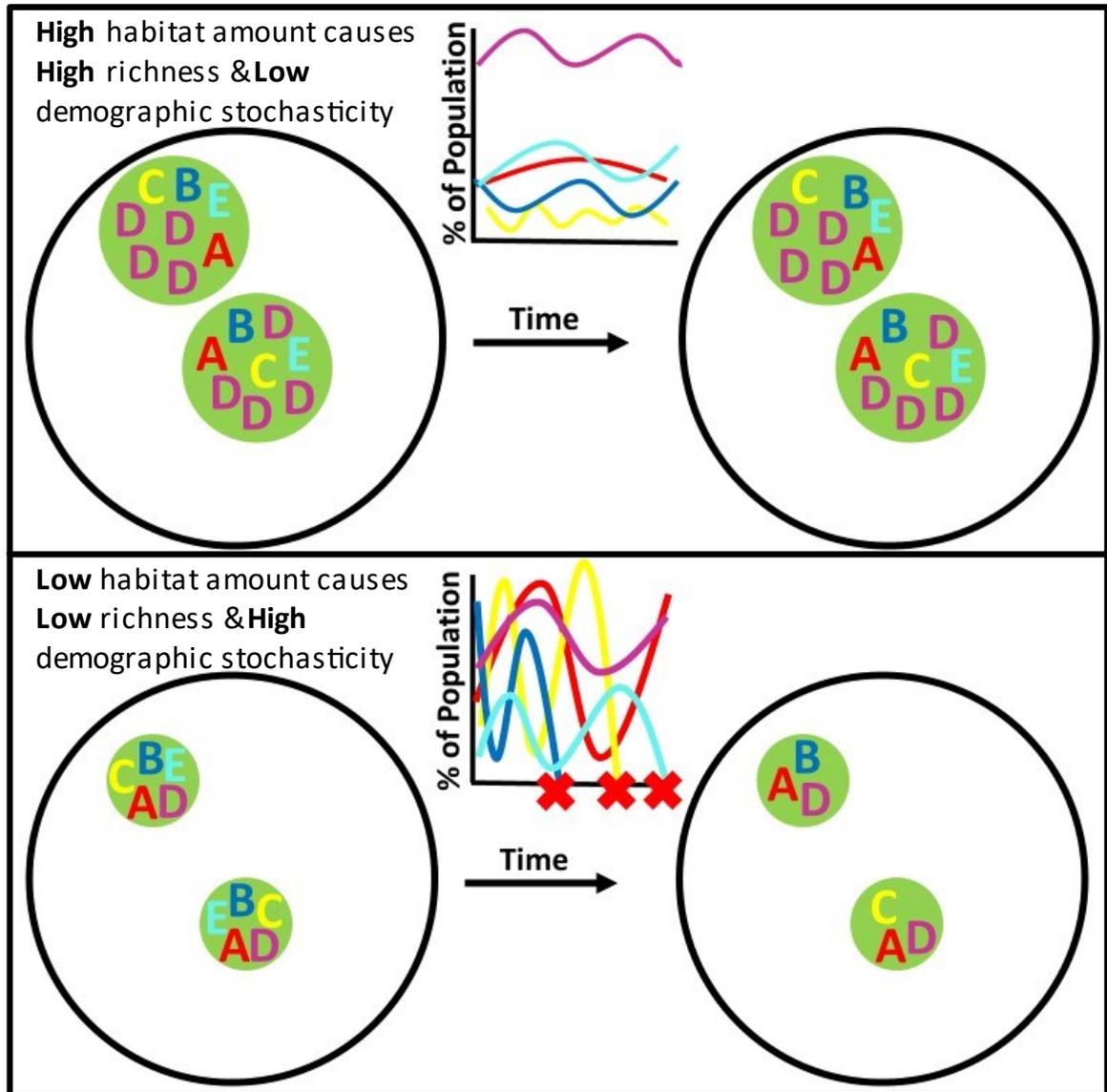


Figure 20. Illustration of explanatory mechanism for observed habitat amount effects on species richness and beta-diversity. Forest patches are green circles, and letters represent hypothetical plant species. Colored lines on graphs indicate fluctuations in population size, with red crosses indicating extirpation of a species. In our example, demographic stochasticity is higher in landscapes with less habitat because population sizes are lower. This could cause lower species richness at an individual site, and higher uniqueness of species assemblages at sites because random fluctuations in population size will have a stronger role in governing species assemblages.

Effects of forest fragmentation

We found negative effects of forest fragmentation on species richness of forest understory plants. We initially speculated that this could be due to negative edge effects, as was assumed by the previous two studies finding the same result (Püttker et al., 2020, Lehtilä, Vinter, and Dinnetz, 2020). If the species in our forest interior plots are less likely to occur in forest edges than forest interiors, then habitat fragmentation would represent loss of habitat for these species. We tested this in two ways. First, we replaced total forest amount with interior forest amount in the model. If an edge effect were responsible for the fragmentation effect, then the fragmentation effect should disappear or be greatly reduced when interior forest amount replaces total forest amount. The effect of fragmentation on species richness decreased only slightly in strength when interior forest amount replaced total forest amount. Second, we tested for an effect of fragmentation on the proportion of forest interior specialists. If a negative edge effect is responsible for the negative fragmentation effect, then we should expect the proportion of forest interior species to decrease with increasing fragmentation. Our results did not strongly support this prediction.

An alternative explanation for the negative fragmentation effect on forest understory plant richness is higher dispersal mortality (rather than low habitat quality at edges) in more fragmented landscapes (Figure 21). For a given amount of forest, a more fragmented landscape has more edge, which will increase the likelihood of seed dispersal into the matrix (Devlaeminck, Bossuyt, and Hermy, 2005). Negative fragmentation effects due to higher dispersal mortality are predicted in single-species simulations with random dispersal (Fahrig, 2001). Our results for the proportion of short-distance seed

dispersers appears to support this suggestion. We found that the proportion of short-distance dispersers was higher in sites surrounded by more fragmented forest. Short-distance dispersers should be more affected by seed mortality from dispersal into the matrix compared to long-distance dispersers because they will be less likely to land on suitable habitat. This would place short-distance dispersers at a relative disadvantage for survival and proliferation in landscapes where the habitat is split into many patches. On the other hand, we also found a negative effect of forest fragmentation on species evenness, which seems to counter the dispersal mortality explanation for negative fragmentation effects on species richness. If fragmentation increases dispersal mortality this should also reduce dispersal success, which should tend to increase evenness as competitive dominants are less likely to dominate in sites in more fragmented landscapes, while we found the opposite.

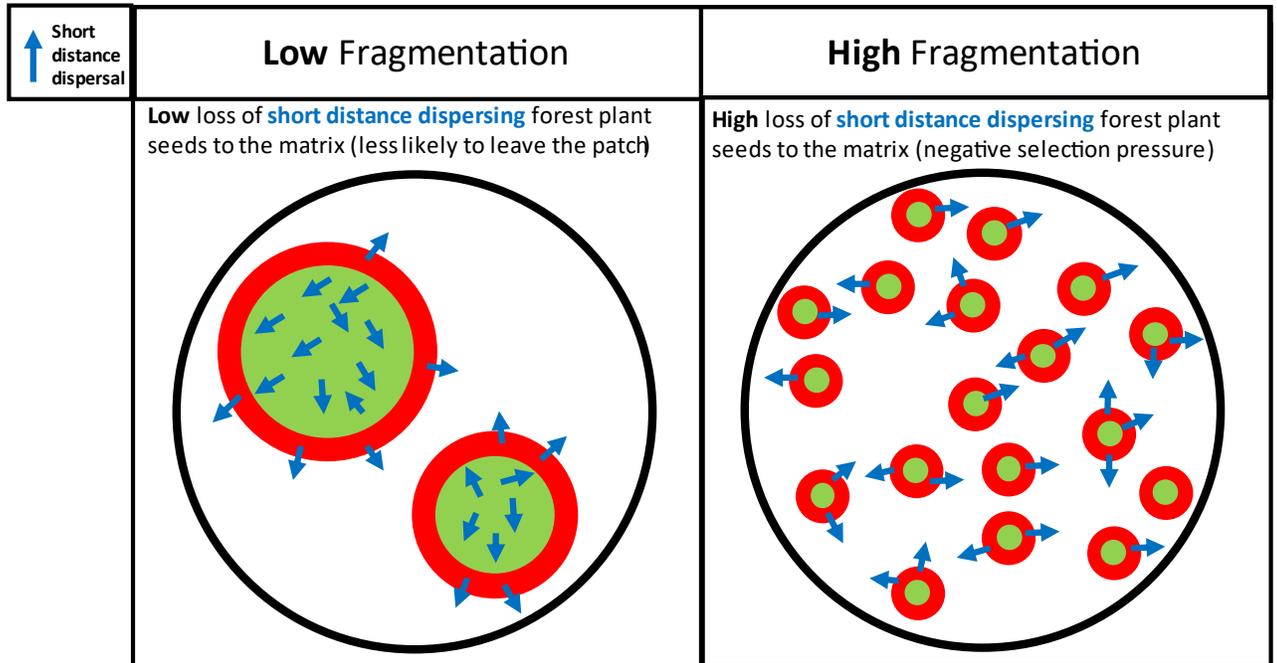


Figure 21. Illustration of explanatory mechanism for fragmentation results. Forest patches are green circles. Arrows represent dispersal/movement, with blue arrows representing dispersal by short distance dispersers, and black arrows represent dispersal by long distance dispersers. Red borders around forest patches represent habitat edges. In landscapes with more fragmentation, edge density is higher, and dispersal across patch boundaries is more common. Short distance dispersers are negatively affected by dispersal into the matrix because they are unable to cross gaps between patches and lose seeds to the matrix at a high rate. Long distance dispersers are less affected by fragmentation because they can successfully disperse between patches.

Uncovering the cause of the negative effect of forest fragmentation on understory plant richness will require further research. Two previous forest plant studies with methods similar to ours also found a negative effect of landscape-scale fragmentation on site-scale forest plant species richness (Püttker et al., 2020, Lehtilä, Vinter, and Dinnetz, 2020). Both of these previous studies attributed these negative effects to negative edge effects, i.e. lower habitat quality at edges for forest specialist species. Our results suggest that such inferences are premature.

Effects of structural connectivity

We found no overall effect of structural connectivity on species richness of understory plants. However, we found negative effects of connectivity on both species evenness and a site's contribution to beta diversity. These results suggest that corridors alter the species composition of forest understory plant communities, to the benefit of some species and at a cost to others, essentially acting as “ecological filters” (Liira and Paal, 2013; Paal, Zobel, and Liira 2020). This is supported by research showing that plant communities in forests and corridors share many species in common (Roy & deBlois, 2006), but tend to differ from each other based on which species are more abundant. Roy & de Blois (2006) found that forest plants with specific functional traits (short distance dispersal and early flowering time) were significantly less abundant in corridors compared to forests. McCollin et al. (2000) found that hedgerows acted as selective filters for forest plants, containing a lower abundance of forest interior plants when compared to forest patches. This could result in increased abundance of corridor dispersing species at more connected forest sites, which could decrease species evenness there (Figure 22). Furthermore, these corridor dispersers might out-compete other species in sites in landscapes with more structural connectivity, reducing the contribution of those sites to beta diversity.

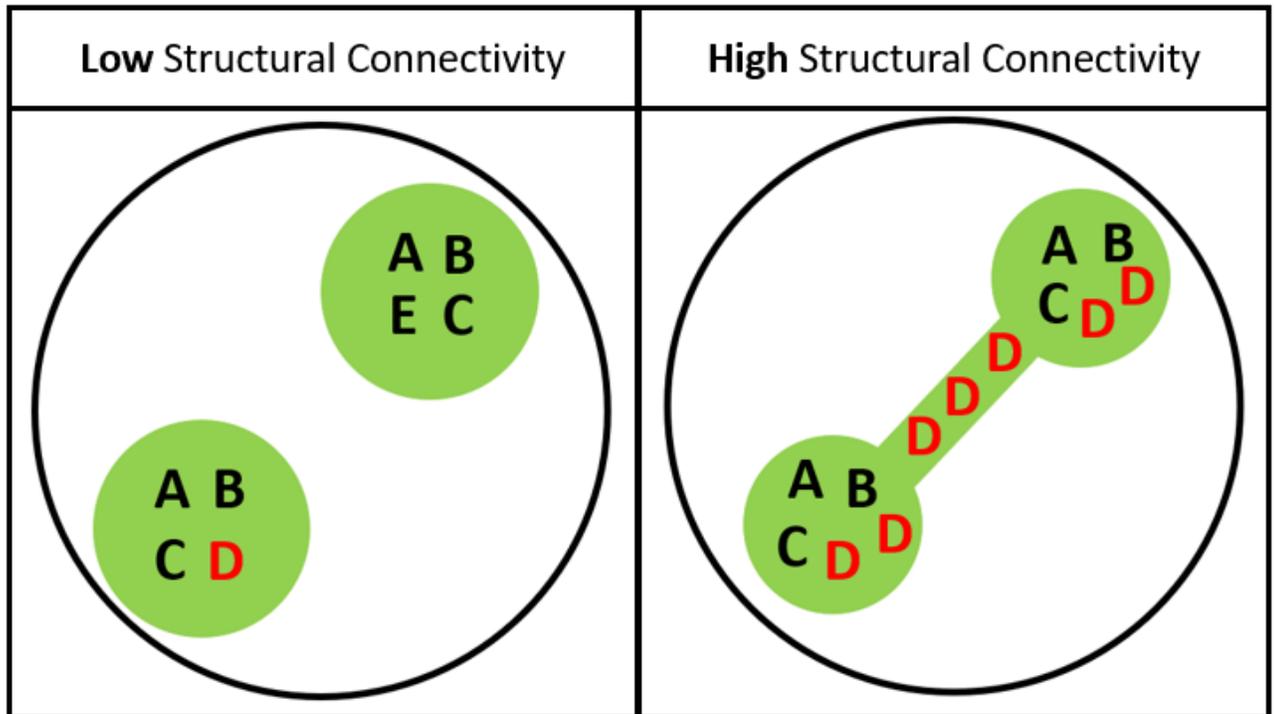


Figure 22. Illustration of potential explanatory mechanism for structural connectivity results. Forest patches are green circles and corridors are green lines. Each letter represents a different hypothetical plant species, with the red species D representing a plant species that can disperse through corridors. This species will proliferate throughout the landscape, which will give it a competitive advantage and increase its population size.

Previous studies have not analyzed the effects of structural connectivity on beta diversity of understory plants in forest patches. However, Calçada et al. (2013) evaluated the role of streams as corridors for forest plants. In that system, streams provide connectivity to the subset of forest plant species whose seeds can be dispersed by water. Similar to our results, Calçada et al. (2013) found that increased structural connectivity via streams resulted in no change in alpha diversity and a decrease in beta diversity. Overall our results on connectivity do not support the assumption that they benefit forest understory plant diversity in general but rather that they alter species composition.

In contrast to our results for forested sites, studies in open environments found higher plant species richness in patches connected to other patches via corridors

(Damschen et al. 2019, Damschen et al. 2006, Damschen et al. 2014). The lack of consistency between our findings and these studies could be attributed to differences in the way that plants respond in the open-habitat environment (Travers, Härdtle, and Matthies, 2021). Open habitat corridors may not act as filters, but rather provide habitat and connectivity for all species found in open-habitat patches. As such, they benefit all or most species in the open-habitat communities. Our results suggest that these previous results in open-environment experiments are not transferable to forested environments and should not be used as support for creation of corridors to maintain forest plant diversity.

Controlling potentially confounding factors:

There are several known confounding factors which could have affected plant species diversity, such as historical site conditions (Finn & Vellend, 2005; Vellend et al., 2007), historical connectivity (Uroy, Ernoult, & Mony 2019), and matrix type (Murphy & Lovett-Doust, 2004). Each of these factors are expected to differ across our study region because of regional land management practices and land use. Through our study design, we have been able to reduce the influence of these factors by mixing different landscape types evenly across the study region and matrix types. This allows the potential influence of these unmeasured confounding factors to be evenly distributed within our statistical models, controlling for covariance between the landscape variables and these unquantified variables. We also found no residual spatial autocorrelation in our models, which further suggests that these factors did not cause issues with interpreting our results under the assumption of normality.

Summary of findings and conservation implications:

Our findings indicate that to increase plant species richness at forest interior sites, one should prioritize the conservation of forest amount in the surrounding landscapes. This effect was stronger and more consistent across scales than any other effect analyzed in this study (forest amount effect size= 1.7x larger than fragmentation; interior amount effect size=2.5x larger than fragmentation). Our results suggest that altering spatial configuration of forest in a landscape is not a substitute for forest preservation and restoration.

Our findings also indicated that increasing conservation of forest in the surrounding landscape can simultaneously reduce the species assemblage uniqueness of a site. Though this may suggest a conservation trade off, decreasing beta-diversity is not necessarily a negative effect. More variable species compositions may have positive or negative effects on communities, depending on whether more unique species are targeted/at risk species (Socolar et al., 2016). Conservation practitioners should analyze species assemblages in isolated sites prior to prioritizing their conservation, since unique species assemblages may not be essential for their conservation goals.

In addition to the positive effect of forest amount, forest fragmentation reduced forest understory plant species richness, with stronger effects on short distance dispersers. If such species are more at risk than long-distance dispersers, this suggests that conservation actions should aim to reduce fragmentation where possible. For example, when a choice is available, forest restoration should occur in sites adjacent to existing forest.

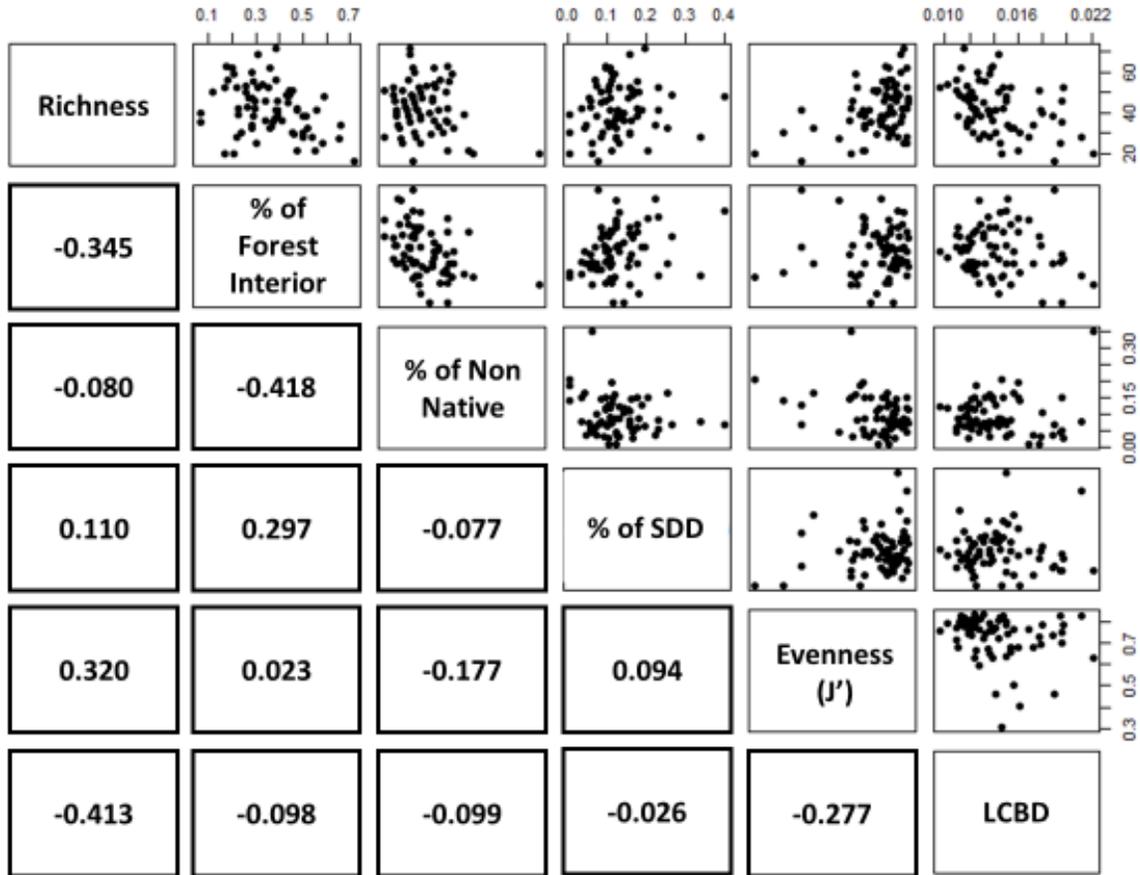
Despite forest edges increasing in fragmented landscapes, fragmentation did not increase the proportion of non-native species in plant communities. This indicates that despite the high abundance of non-native species in forest edges (Cadotte and Lovett-Doust, 2001), fragmentation is not promoting the spill-over of these species into forest interiors.

Structural connectivity did not affect forest understory plant species richness and resulted in decreases in both species evenness and a site's contribution to beta diversity. Our findings therefore do not support prioritizing the conservation of hedgerows for the purpose of maintaining or increasing biodiversity of forest understory plants.

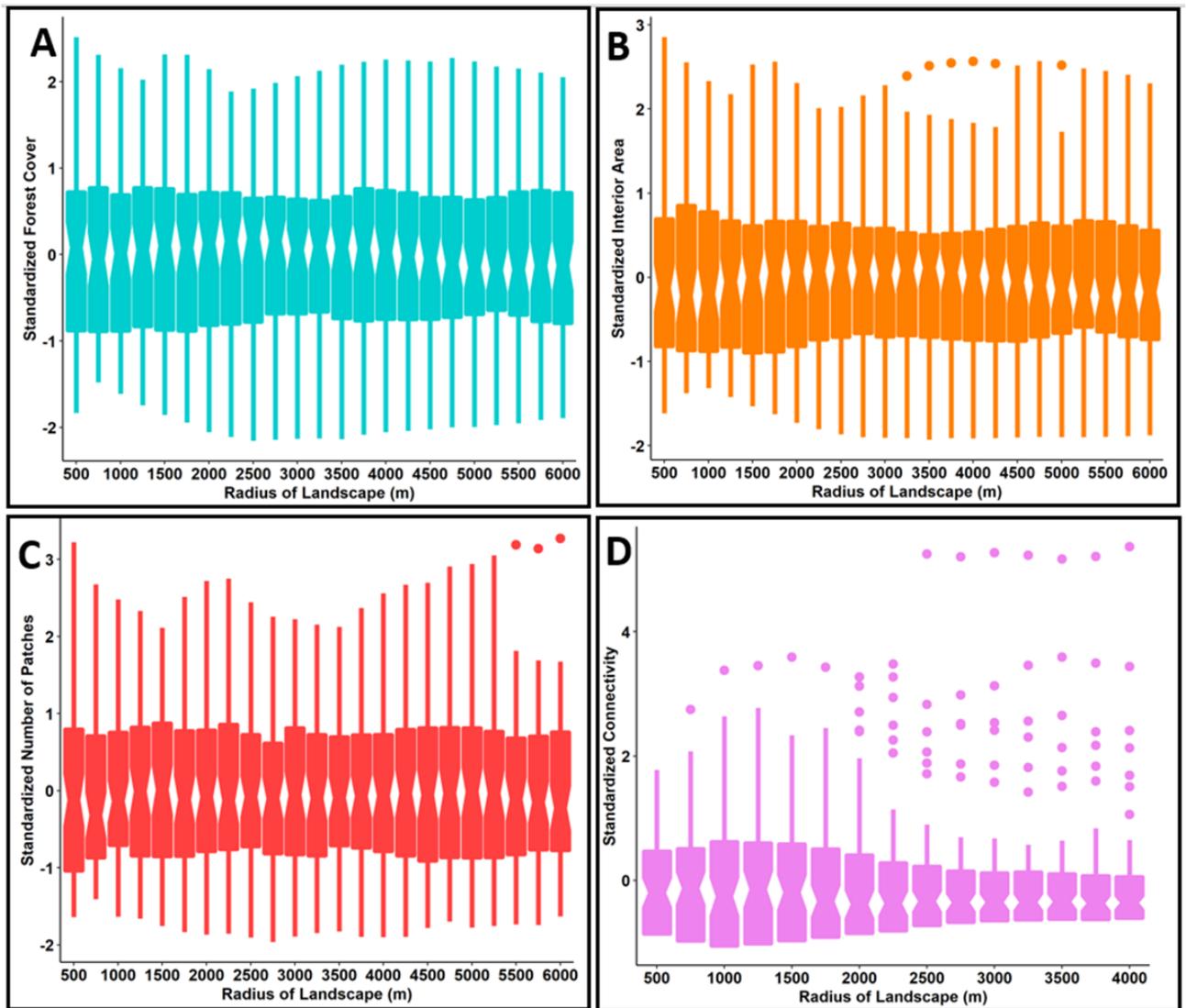
Nonetheless, hedgerows do provide important habitat for a wide variety of species, which can greatly increase biodiversity in agricultural landscapes (Garratt, 2017; Hannon and Sisk, 2009; Travers, Härdtle, and Matthies, 2021; Hinsley and Bellamy, 2000; Sirami et al. 2019).

In summary, ours is the first study to evaluate the independent effects of forest amount, forest fragmentation, and structural connectivity on understory plant species richness. We find strong positive effects of forest amount and negative effects of forest fragmentation but no effect of structural connectivity. Maintenance of forest understory plant species diversity is therefore best accomplished by the conservation and restoration of forest wherever possible, and when choice is available, restoration of forest should be done adjacent to existing forest.

Appendix:



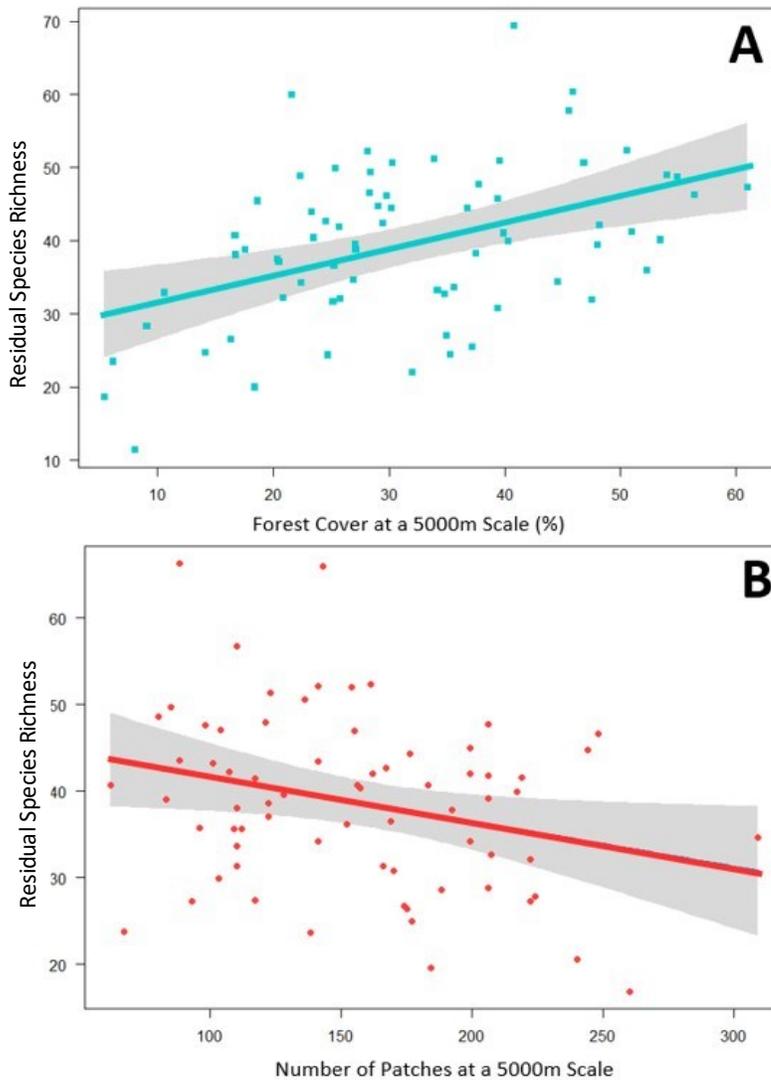
Appendix Figure 1. Correlation matrix with scatterplots and spearman correlation values (r) for all response variables estimated in our study. Each point in the scatterplots represents the response variable values for one of 70 sites sampled for forest understory plant diversity. Richness is the plant species richness of the site after sampling 184 m² of the forest understory. “% of forest interior” is the proportion of species at a forest site that are “forest interior specialists”, meaning they are only described as occurring in forest interiors in regional floras. “% of Non Native” is the proportion of species at a forest site that are not native to the study region. “% of SDD” is the proportion of species at a forest site that are short distance dispersers (i.e. primary dispersal type=unassisted, explosive, water, or ants). Evenness (J') is the species evenness at forest sites. LCBD is the local contribution to beta diversity, which is a measure of the site scale species assemblage uniqueness relative to all 70 sites.



Appendix Figure 2. Distribution of predictor variables at all spatial extents considered in models. Boxplots show the variance of standardized values in the models, and points indicate outliers. For structural connectivity boxplots, only the 750-2500m scales were analyzed because beyond this point, values become highly skewed. Each boxplot shows the standardized range of values present in the response variables at a particular landscape size.

Appendix Table 1. Model outputs for generalized linear models with binomial distribution that tested the relationship between the response (species richness) and landscape predictors at their scale of maximum effect (forest amount, fragmentation as number of patches, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for scales between 500-6000m, with the extent being increased by 250m for each new model tested. Structural connectivity was only included in the model from a 750 – 2500 m scale. These models were used to test the independent effect of each landscape variable on plant species richness. The forest amount variable measures the amount of forest habitat in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). Model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

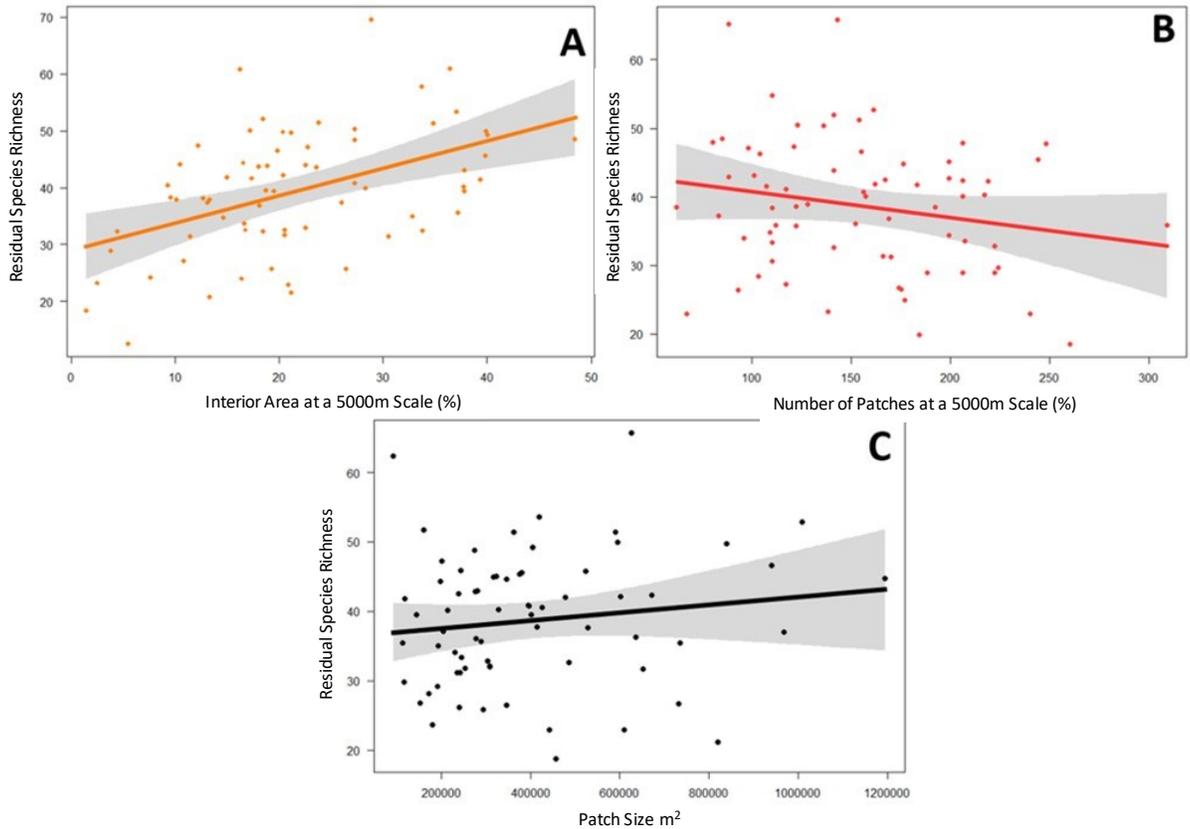
Species Richness		
<i>Predictors</i>	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	4.0193	4.0887 to 3.9599
Forest Amount 5000m	0.11614	0.17551 to 0.056772
Fragmentation 5000m	-0.06782	-0.00857 to -0.12707
<i>Structural Connectivity 2500m</i>	0.003595	0.06793 to -0.6074
Wetness Index	-0.11091	-0.05218 to -0.16963
Canopy Closure [>60%]	-0.31442	-0.003035 to -0.62581
Observations	70	
Pseudo R ² (Nagelkerke)	0.568	
AIC	528.88	



Appendix Figure 3. Scatterplots of relationship between residual forest understory plant species richness and forest amount (**A**) and fragmentation per se (number of patches; **B**) at their scale of maximum effect after all other variables in models are controlled for (model described in **Table A2**). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for scales between 500-6000m, with the extent being increased by 250m for each new model tested. These models were used to test the independent effect of each landscape variable on plant species richness. The forest amount variable measures the amount of forest habitat in the landscape. Fragmentation per se variable measures the number of patches in the landscape. Model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All regression plots were made using the “visreg” package in R.

Appendix Table 2. Model outputs for generalized linear models with binomial distribution that tested the relationship between understory plant species richness and landscape predictors at their scale of maximum effect (interior amount, fragmentation as number of patches, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for scales between 500-6000m, with the extent being increased by 250m for each new model tested. Structural connectivity was only included in the model from a 750 – 2500 m scale. These models were used to test the independent effect of each landscape variable on plant species richness. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). Model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

<i>Predictors</i>	Species Richness	
	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	4.05021	4.3571 to 3.7433
Interior amount 5000m	0.12489	0.18547 to 0.064306
Fragmentation per se 5000m	-0.04954	0.011808 to -0.11089
<i>Structural Connectivity 2500m</i>	<i>0.009826</i>	<i>0.072893 to -0.05324</i>
Wetness Index	-0.11117	-0.053115 to -0.16922
Canopy Closure [>60%]	-0.34674	-0.65365 to -0.039823
Observations	70	
Pseudo R ² (Nagelkerke)	0.584	
AIC	527.55	



Appendix Figure 4. Scatterplots of relationship between residual species richness and variables in interior amount models at their scale of maximum effect after all other variables in models are controlled for. The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for scales between 500-6000m, with the extent being increased by 250m for each new model tested. These models were used to test the independent effect of each landscape variable on plant species richness. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. Patch size is the size of the focal patch where surveys were conducted. Model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. (A) shows the relationship between species richness and interior amount (at a 5000m scale). (B) shows the relationship between species richness and number of patches (at a 5000m scale). (C) shows the relationship between species richness and patch size (in m²). The relationship between species richness and interior amount was the only significant landscape or patch scale predictor in the is model (shown in **Table A5**). All regression plots were made using the “visreg” package in R.

Appendix Table 3. Model outputs for beta regression models that tested the relationship between the proportion of non-native plant species at a forest site and landscape predictors at their scale of maximum effect for species richness (interior amount, fragmentation per se, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

<i>Predictors</i>	Proportion of Non-Native	
	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	-1.59306	-2.25418; -0.9319
Interior amount 2500m	-0.13736	0.0065236 to -0.28124
Fragmentation per se 2500m	-0.03194	-0.17159 to 0.10771
Structural Connectivity 2500m	0.08523	-0.05442 to 0.22488
Wetness Index	-0.02888	-0.16853 to 0.11077
Canopy Closure [>60%]	-0.58779	-1.28257 to 0.10699
Observations	70	
R ²	0.092	

Appendix Table 4. Model outputs for beta regression models that tested the relationship between the proportion of non-native plant species at a forest site and landscape predictors at their scale of maximum effect in species richness models (interior amount and fragmentation per se). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

Proportion of Non-Native		
<i>Predictors</i>	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	-1.61610	-2.277634; -0.95456
Interior amount 5000m	-0.07677	-0.2295912; 0.0760512
Fragmentation per se 5000m	0.07754	-0.0752812; 0.2303612
Wetness Index	-0.04715	-0.1999712; 0.1056712
Canopy Closure [>60%]	-0.67983	-1.3562652; -0.0033948
Observations	70	
R ²	0.066	

Appendix Table 5. Model outputs for beta regression models that tested the relationship between the proportion of forest interior plant species specialists at a site and landscape predictors at their scale of maximum effect in species richness models (interior amount, fragmentation per se as number of patches, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. Species were categorized as “forest interior specialists” if floras for the study region only described them as living in forests or treed swamps (not including edges). sAll standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

Proportion of Forest Interior Specialists		
<i>Predictors</i>	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	-1.51577	-2.25416; -0.77737
Interior amount 2500m	0.01266	-0.09512; 0.120440
Fragmentation per se 2500m	-0.03904	-0.14682; 0.06874
Structural Connectivity 2500m	0.05952	-0.04826; 0.16730
Wetness Index	0.40024	0.29245; 0.50802
Canopy Closure [>60%]	0.80845	0.06216; 1.55473
Observations	70	
R ²	0.485	

Appendix Table 6. Model outputs for beta regression models that tested the relationship between the proportion of forest interior plant species specialists at a site and landscape predictors at their scale of maximum effect in species richness models (interior amount and fragmentation per se as number of patches). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. Species were categorized as “forest interior specialists” if floras for the study region only described them as living in forests or treed swamps (not including edges). All standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

<i>Predictors</i>	Proportion of Forest Interior Specialists	
	<i>Estimates</i>	<i>CI</i>
(Intercept)	-1.421750	-2.1467; -0.69677
Interior amount 5000m	0.021372	-0.09192; 0.134667
Fragmentation per se 5000m	-0.003974	-0.11727; 0.109321
Wetness Index	0.402408	0.28911; 0.51570
Canopy Closure [>60%]	0.712689	-0.019839; 1.44522
Observations	70	
R ²	0.475	

Appendix Table 7. Model outputs for beta regression models that tested the relationship between the proportion of short distance dispersed plant species at a site and landscape predictors at their scale of maximum effect in species richness models (interior amount, fragmentation per se as number of patches, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. Dispersal distance categories were derived from plant species dispersal type, where “Wind” or “Animal” dispersal were considered long distance dispersal types, and “Unassisted”, “Ants”, “Explosive”, and “Water” were considered short distance dispersal types. All standardized effect sizes are shown as incidence rate ratios. 95% confidence intervals are shown.

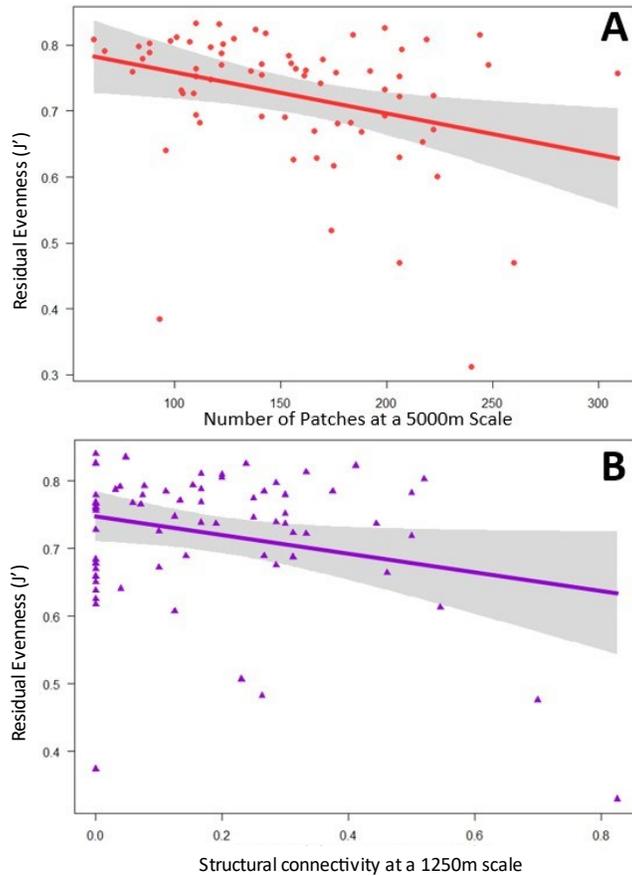
<i>Predictors</i>	Proportion of Short Distance Dispersers	
	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	-2.03921	-2.8818; -1.19655
Interior amount 2500m	-0.08878	-0.2299; 0.05234
Fragmentation per se 2500m	-0.22545	-0.37188; -0.07902
Structural Connectivity 2500m	0.09162	-0.05048; 0.23372
Wetness Index	0.06405	-0.0802; 0.2083
Canopy Closure [>60%]	0.09151	-0.76109; 0.94411
Observations	70	
R ²	0.110	

Appendix Table 8. Model outputs for beta regression models that tested the relationship between the proportion of short distance dispersed plant species at a site and landscape predictors at their scale of maximum effect in species richness models (interior amount and fragmentation per se as number of patches). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. The interior amount variable measures the amount of interior forest habitat (forested areas >30m from forest edges) in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. Dispersal distance categories were derived from plant species dispersal type, where “Wind” or “Animal” dispersal were considered long distance dispersal types, and “Unassisted”, “Ants”, “Explosive”, and “Water” were considered short distance dispersal types. All standardized effect sizes are shown as incidence rate ratios. 95%confidence intervals are shown.

<i>Predictors</i>	Proportion of Short Distance Dispersers	
	<i>Estimates</i>	<i>CI</i>
(Intercept)	-1.93281	-2.76847; -1.09715
Interior amount 5000m	0.01327	-0.13801; 0.16279
Fragmentation per se 5000m	-0.17704	-0.3351; -0.01895
Wetness Index	0.07062	-0.080457; 0.221697
Canopy Closure [>60%]	-0.01019	-0.85669; 0.8566
Observations	70	
R ²	0.0801	

Appendix Table 9. Model outputs for beta regression models that tested the relationship between plant species evenness (as J') and landscape predictors at their scale of maximum effect (forest amount, fragmentation as number of patches, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for scales between 500-6000m, with the extent being increased by 250m for each new model tested. These models were used to test the independent effect of each landscape variable on forest understory plant species evenness. The forest amount variable measures the amount of forest habitat in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All standardized effect sizes are shown as incidence rate ratios. 95% confidence intervals are shown.

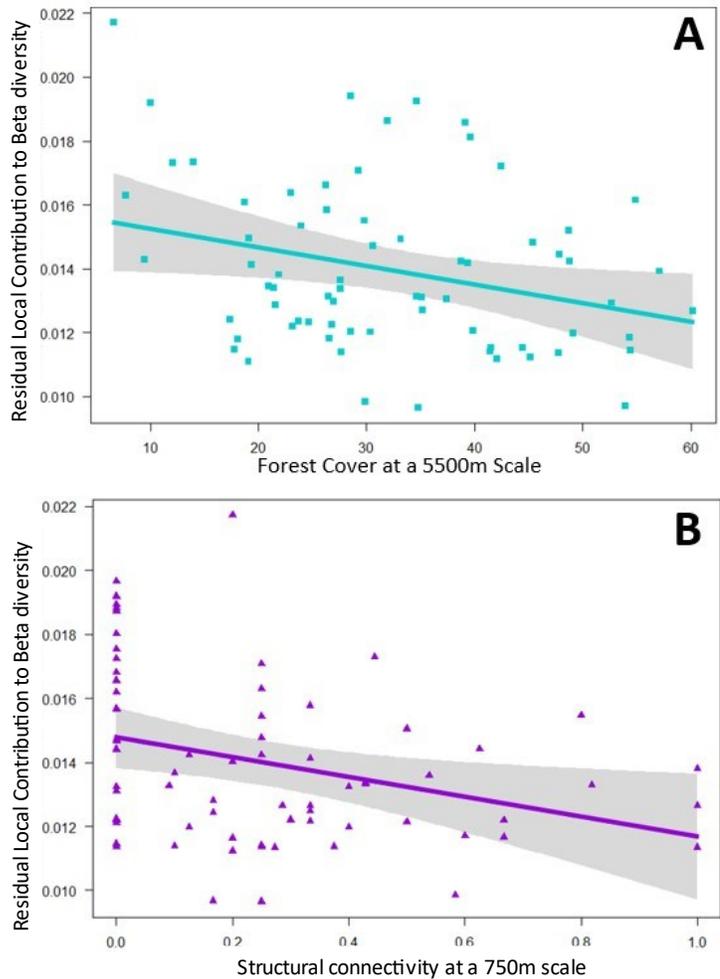
<i>Predictors</i>	Species Evenness (J')	
	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	0.700041	0.557550 to 0.842532
Forest Amount 5000m	-0.005806	-0.031372 to 0.019759
Fragmentation per se 5000m	-0.032616	-0.057820 to -0.007412
<i>Structural Connectivity 1500m</i>	-0.024633	-0.04994 to 0.000675
Wetness Index	-0.009121	-0.034612 to 0.016369
Canopy Closure [$>60\%$]	0.026888	-0.117710 to 0.171486
Observations	70	
R^2 / R^2 adjusted	0.118 / 0.063	
AIC	-116.522	



Appendix Figure 5. Scatterplots of relationship between residual species evenness (J') and significant landscape variables at their scale of maximum effect after all other variables in models are controlled for. The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for all scales between 500-6000m for bivariate models with forest habitat amount and fragmentation per se considered, and 750-2500m scale for trivariate models with structural connectivity included as well. Models were tested at multiple different landscape extents, with the extent being increased by 250m for each new model tested. These models were used to test the independent effect of each landscape variable on plant species evenness. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). Model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. (A) shows the relationship between evenness and number of patches (at a 5000m scale). (B) shows the relationship between evenness and structural connectivity (at a 1250m scale) (Full model details outlined in **Table A12 & A13**). All regression plots were made using the “visreg” package in R.

Appendix Table 10. Model outputs for general linear models that tested the relationship between the response local contribution to beta diversity and landscape predictors at their scale of maximum effect (forest amount, fragmentation, and structural connectivity). The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for scales between 500-6000m, with the extent being increased by 250m for each new model tested. Structural connectivity was only included in the model from a 750–2500 m scale. These models were used to test the independent effect of each landscape variable on local contribution to beta diversity. The forest amount variable measures the amount of forest habitat in the landscape. Fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). The model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. All standardized effect sizes are shown as incidence rate ratios. 95% confidence intervals are shown.

LCBD		
<i>Predictors</i>	<i>Estimates</i>	<i>95% CI</i>
(Intercept)	0.013888	0.010255 to 0.017520
Forest Amount 5500m	-0.000760	-0.001422 to -0.000098
Fragmentation per se 5500m	0.000097	-0.000555 to 0.000749
Structural Connectivity 750m	-0.000833	-0.001500 to -0.000166
Wetness Index	-0.000798	-0.001450 to -0.000147
Canopy Closure [>60%]	0.000410	-0.003276 to 0.004096
Observations	70	
R ² / R ² adjusted	0.197 / 0.148	
AIC	-630.24	



Appendix Figure 6. Scatterplots of relationship between local contribution to beta diversity (LCBD) and significant landscape variables at their scale of maximum effect after all other variables in models are controlled for. The scale of maximum effect was the landscape extent where the delta AIC value was lowest for the model, indicating the most parsimonious model. Models were tested for all scales between 500-6000m for bivariate models with forest habitat amount and fragmentation per se considered, and 750-2500m scale for trivariate models with structural connectivity included as well. Models were tested at multiple different landscape extents, with the extent being increased by 250m for each new model tested. The fragmentation per se variable measures the number of patches in the landscape. The structural connectivity variable measures the extent to which patches are connected to one another via woody corridors (linear woody patches <30m in width). Model also included two site scale variables used to control for site scale variation: a wetness index that measures the moisture level of the site, and a binary canopy closure variable that differentiates between sites with tree canopy cover above or below 60%. **(A)** shows the relationship between forest amount and LCBD (at a 5500m scale). **(B)** shows the relationship between structural connectivity and LCBD (at a 750m scale). All regression plots were made using the “visreg” package in R.

Appendix Table 11. Species list that has information on native status, habitat preference, primary dispersal syndrome, and cover. “Y” for native status means a species is native, “N” means a species is non-native, and “NA” means a species was not classified (because identification was not down to the species level). For habitat preference, “Y” means the species is only found in forests or treed swamp interiors, “N” means the species is found in edge or open environments, and “NA” means a species could not be classified (because identification was not down to the species level). Primary dispersal type is shown, where “Wind” or “Animal” dispersal were considered long distance dispersal types, and “Unassisted”, “Ants”, “Explosive”, and “Water” were considered short distance dispersal types. “NA” means the species could not be classified because no data could be found for dispersal type.

Species	Native?	Forest Interior Specialist?	Primary Dispersal Type	Cover Over All Sites
<i>Abies balsamea</i>	Y	Y	Wind	322.5
<i>Acer negundo</i>	Y	N	Wind	37.75
<i>Acer nigrum</i>	Y	Y	Wind	63.5
<i>Acer pensylvanicum</i>	Y	Y	Wind	6
<i>Acer rubrum</i>	Y	N	Wind	683.5
<i>Acer saccharinum</i>	Y	N	Wind	261.25
<i>Acer saccharum</i>	Y	N	Wind	3565.25
<i>Acer spicatum</i>	Y	N	Wind	12
<i>Actaea pachypoda</i>	Y	Y	Animal	61
<i>Actaea rubra</i>	Y	Y	Animal	86.75
<i>Adiantum pedatum</i>	Y	Y	Wind	109.75
<i>Ageratina altissima</i>	Y	N	Wind	5
<i>Agrimonia gryposepala</i>	Y	N	Animal	34
<i>Alliaria petiolata</i>	N	N	Unassisted	495.5
<i>Allium tricoccum</i>	Y	Y	Animal	351.75
<i>Alnus incana</i>	Y	N	Wind	7
<i>Amelanchier</i> spp.	NA	NA	NA	185.25
<i>Amphicarpaea bracteata</i>	Y	N	Unassisted	57.25
<i>Anemone virginiana</i>	Y	N	Wind	20
<i>Apocynum</i> spp.	Y	N	Wind	13
<i>Aralia nudicaulis</i>	Y	N	Animal	943.75
<i>Arctium minus</i>	N	N	Animal	11
<i>Arisaema triphyllum</i>	Y	N	Animal	360
<i>Asarum canadense</i>	Y	Y	Ants	96.75
<i>Asplenium viride</i>	Y	Y	Wind	1
<i>Athyrium filix-femina</i>	Y	N	Wind	1292.75
<i>Betula alleghaniensis</i>	Y	N	Wind	28.5
<i>Betula papyrifera</i>	Y	N	Wind	66.75
<i>Betula populifolia</i>	Y	N	Wind	5
<i>Bidens frondosa</i>	Y	N	Animal	1
<i>Bidens tripartita</i>	Y	N	Animal	3
<i>Boehmeria cylindrica</i>	Y	Y	NA	94.5
<i>Botrychium virginianum</i>	Y	Y	Wind	24
<i>Caltha palustris</i>	Y	N	Water	8.5
<i>Cardamine bulbosa</i>	Y	Y	Explosive	3.5
<i>Cardamine diphylla</i>	Y	Y	Explosive	55.5
<i>Carex plantaginea</i>	Y	Y	Unassisted	173.5
<i>Carex</i> spp.	NA	NA	NA	3723.75
<i>Carpinus caroliniana</i>	Y	Y	Wind	372
<i>Carya cordiformis</i>	Y	Y	Animal	574.5
<i>Caulophyllum giganteum</i>	Y	Y	Animal	1462
<i>Celastrus scandens</i>	Y	N	Animal	22.75
<i>Celtis occidentalis</i>	Y	N	Animal	3
<i>Chelone glabra</i>	Y	N	NA	27
<i>Circaea alpina</i>	Y	Y	Animal	14
<i>Circaea canadensis</i>	Y	N	Animal	670.75
<i>Cirsium</i> spp.	NA	NA	NA	2

Claytonia virginica	Y	N	Ants	11.5
Clematis virginiana	Y	N	Wind	66.5
Clinopodium vulgare	Y	N	Unassisted	7
Clintonia borealis	Y	Y	Animal	186
Coptis trifolia	Y	Y	Unassisted	246.75
Cornus alternifolia	Y	N	Animal	491.5
Cornus canadensis	Y	N	Animal	29.5
Cornus racemosa	Y	N	Animal	42.75
Cornus sericea	Y	N	Animal	10
Corylus cornuta	Y	N	Animal	531.75
Crataegus spp.	NA	NA	NA	42.75
Cypripedium acaule	Y	N	NA	2
Cystopteris bulbifera	Y	Y	Wind	4
Dalibarda repens	Y	Y	Animal	16
Dendrolycopodium dendroideum	Y	N	Wind	345.75
Dicentra canadensis	Y	Y	Ants	8
Dicentra cucullaria	Y	Y	Ants	36.25
Diervilla lonicera	Y	N	NA	68
Diphasiastrum digitatum	Y	N	Wind	270.75
Dirca palustris	Y	Y	Animal	79.5
Dryopteris carthusiana	Y	Y	Wind	507.5
Dryopteris clintoniana	Y	N	Wind	3
Dryopteris cristata	Y	N	Wind	17
Dryopteris intermedia	Y	Y	Wind	17.5
Dryopteris marginalis	Y	Y	Wind	28.25
Dryopteris goldieana	Y	Y	Wind	1
Echinocystis lobata	Y	N	Animal	2
Elymus hystrix	Y	Y	Animal	144
Epipactis helleborine	N	N	Wind	228
Equisetum arvense	Y	N	Wind	30
Equisetum hyemale	Y	N	Wind	47.75
Equisetum scirpoides	Y	Y	Wind	95
Equisetum sylvaticum	Y	N	Wind	17.5
Erigeron philadelphicus	Y	N	Wind	8
Erythronium americanum	Y	Y	Ants	1560.25
Euonymus obovatus	Y	Y	Animal	2
Eurybia macrophylla	Y	Y	Animal	29.75
Eutrochium maculatum	Y	N	Wind	3
Fagus grandifolia	Y	Y	Animal	689.25
Fallopia cilinodis	Y	N	NA	2
Fragaria virginiana	Y	N	Animal	258.75
Frangula alnus	N	N	Animal	1875.25
Fraxinus americana	Y	Y	Wind	1862.5
Fraxinus nigra	Y	Y	Wind	740
Fraxinus pennsylvanica	Y	N	Wind	586.75
Galium aparine	Y	N	Animal	20.5
Galium asprellum	Y	N	Animal	23.25
Galium circaeans	Y	Y	Animal	10
Galium palustre	Y	N	Animal	41.75
Galium spp.	NA	NA	NA	12
Galium triflorum	Y	N	Animal	245.75
Gaultheria procumbens	Y	N	Animal	76.25
Geranium robertianum	Y	N	Explosive	23.25
Geum canadense	Y	N	Animal	221.75
Geum fragarioides	Y	N	Animal	62.25
Geum laciniatum	Y	N	Animal	3
Geum urbanum	N	N	Animal	139.75
Gymnocarpium dryopteris	Y	Y	Wind	41.75
Hepatica acutiloba	Y	N	Ants	50.5
Pilosella caespitosa	N	N	Wind	4
Pilosella piloselloides	N	N	Wind	6
Huperzia lucidula	Y	Y	Wind	1
Hydrophyllum virginianum	Y	Y	Water	106.25
Ilex verticillata	Y	N	Animal	309.75
Impatiens capensis	Y	N	Explosive	25
Juglans cinerea	Y	Y	Animal	1
Juniperus communis	Y	N	Animal	3
Lactuca biennis	Y	N	Wind	5.5
Lactuca spp.	NA	N	Wind	4

Laportea canadensis	Y	Y	Unassisted	41.5
Lobelia inflata	Y	N	Unassisted	3
Lonicera canadensis	Y	N	Animal	220
Lonicera dioica	Y	N	Animal	5
Lonicera maackii	N	N	Animal	9.75
Lonicera morrowii	N	N	Animal	30.25
Lonicera tartarica	N	N	Animal	26.75
Lonicera villosa	Y	N	Animal	3
Lycopodium clavatum	Y	N	Wind	62
Lycopus americanus	Y	N	Water	3
Lycopus uniflorus	Y	N	Water	33.75
Lysimachia borealis	Y	Y	Water	232.5
Lysimachia ciliata	Y	N	Water	46.25
Lysimachia nummularia	N	N	Water	26.5
Lythrum salicaria	N	N	Water	3
Maianthemum canadense	Y	Y	Animal	2906.25
Maianthemum racemosum	Y	Y	Animal	770
Malus pumila	N	N	Animal	69.25
Matteuccia struthiopteris	Y	N	Wind	265
Medeola virginiana	Y	Y	NA	80.25
Menispermum canadense	Y	Y	Animal	8
Mitchella repens	Y	N	Animal	463.75
Mitella diphylla	Y	Y	Water	16.75
Monotropa uniflora	Y	Y	Animal	3
Nabalus spp.	NA	NA	NA	110.5
Oclemena acuminata	Y	Y	NA	10.5
Onoclea sensibilis	Y	N	Wind	2292.25
Orthilia secunda	Y	N	NA	10
Osmorhiza claytonii	Y	Y	Wind	4
Osmunda regalis	Y	Y	Wind	379.75
Osmundastrum cinnamomeum	Y	N	Wind	946.25
Ostrya virginiana	Y	Y	Wind	1152.5
Oxalis acetosella	Y	Y	NA	3
Oxalis stricta	Y	N	Explosive	107
Parathelypteris noveboracensis	Y	N	Wind	198.25
Parthenocissus inserta	Y	N	Animal	454.75
Parthenocissus quinquefolia	Y	N	Animal	520.5
Penstemon digitalis	Y	N	NA	2
Persicaria virginiana	Y	Y	Explosive	6
Phegopteris hexagonoptera	Y	N	Wind	40.5
Phlox divaricata	Y	N	Explosive	13.75
Picea glauca	Y	Y	Wind	14
Pilea pumila	Y	N	Water	2
Pinus strobus	Y	N	Wind	25.5
Plantago major	N	N	Animal	2
Poaceae spp.	NA	NA	NA	64
Polygonatum pubescens	Y	N	Animal	72.5
Polystichum arcostichoides	Y	Y	Wind	2
Populus grandidentata	Y	N	Wind	39.5
Populus tremuloides	Y	N	Wind	196.25
Potentilla simplex	Y	N	NA	11
Prunella vulgaris	Y	N	Unassisted	19
Prunus serotina	Y	N	Animal	799.75
Prunus virginiana	Y	N	Animal	1235.5
Pteridium aquilinum	Y	N	Wind	339
Pyrola elliptica	Y	Y	NA	805.75
Quercus alba	Y	N	Animal	43
Quercus macrocarpa	Y	Y	Animal	85.5
Quercus rubra	Y	Y	Animal	82.25
Ranunculus abortivus	Y	N	NA	81.25
Ranunculus pensylvanicus	Y	N	NA	9
Ranunculus recurvatus	Y	N	NA	9
Rhamnus cathartica	N	N	Animal	1750.25
Rhus typhina	Y	N	Animal	3
Ribes americanum	Y	N	Animal	69
Ribes cynosbati	Y	N	Animal	451.5
Ribes hirtellum	Y	N	Animal	70.75
Ribes triste	Y	N	Animal	51.25
Rubus allegheniensis	Y	N	Animal	71.5
Rubus hispida	Y	N	Animal	111.25

Rubus idaeus	Y	N	Animal	165.5
Rubus occidentalis	Y	N	Animal	42.25
Rubus odoratus	Y	N	Animal	26.25
Rubus pubescens	Y	N	Animal	1501.25
Sambucus canadensis	Y	N	Animal	6
Sambucus racemosa	Y	N	Animal	45
Sanguinaria canadensis	Y	N	Animal	25.5
Sanicula marilandica	Y	Y	Animal	8
Scutellaria lateriflora	Y	N	NA	13
Smilax herbacea	Y	N	Animal	6
Smilax hispida	Y	N	Animal	1
Solanum dulcamara	N	N	Animal	24
Solidago altissima	Y	N	Wind	3
Solidago caesia	Y	N	Wind	7
Solidago flexicaulis	Y	Y	Wind	150.75
Solidago spp.	NA	NA	NA	195
Sorbus decora	Y	N	Animal	28.25
Spiraea alba	Y	N	NA	34.5
Streptopus lanceolatus	Y	N	NA	17.75
Symphyotrichum spp.	NA	NA	NA	297.25
Symphyotrichum lateriflorum	Y	N	Wind	71.5
Symplocarpus foetidus	Y	Y	Animal	1
Syringa vulgaris	N	N	NA	3
Taraxacum officinale	N	N	Wind	101.25
Taxus canadensis	Y	Y	Animal	58.75
Thalictrum dioicum	Y	Y	Unassisted	10
Thelypteris palustris	Y	N	Wind	53
Thuja occidentalis	Y	N	Wind	147.5
Tiarella cordifolia	Y	N	Unassisted	206.75
Tilia americana	Y	Y	Wind	523
Toxicodendron rydbergii	Y	N	Ants	835.75
Trillium cernuum	Y	Y	Ants	12.5
Trillium erectum	Y	Y	Ants	76.25
Trillium grandiflorum	Y	Y	Ants	771.5
Trillium undulatum	Y	Y	Ants	10.5
Triosteum aurantiacum	Y	N	NA	6
Tsuga canadensis	Y	N	Wind	84.25
Ulmus americana	Y	N	Wind	4
Uvularia grandiflora	Y	N	Ants	18.5
Uvularia sessilifolia	Y	N	Ants	11
Vaccinium angustifolium	Y	N	Animal	3
Vaccinium myrtilloides	Y	N	Animal	105.5
Valeriana officinalis	N	N	NA	1
Veronica americana	Y	N	Water	10
Veronica officinalis	N	N	Animal	41.5
Veronica serpyllifolia	N	N	NA	12.5
Viburnum acerifolium	Y	N	Animal	12
Viburnum lantanoides	Y	Y	Animal	5
Viburnum lentago	Y	N	Animal	252
Viburnum nudum	Y	N	Animal	152.75
Viburnum rafinesqueanum	Y	N	Animal	1
Viburnum recognitum	Y	N	Animal	3
Viburnum opulus ssp. trilobum	Y	N	Animal	40.75
Vincetoxicum rossicum	N	N	Wind	3
Viola blanda	Y	Y	Ants	1
Viola canadensis	Y	Y	Ants	142.25
Viola cucullata	Y	N	Ants	15.75
Viola labradorica	Y	N	Ants	6
Viola pubescens	Y	Y	Ants	154
Viola renifolia	Y	N	Ants	3
Viola selkirkii	Y	N	Ants	2.5
Viola sororia	Y	N	Ants	39.5
Viola spp.	NA	NA	NA	52
Vitis riparia	Y	N	Animal	238.75
Zanthoxylum americanum	Y	N	Animal	973.5

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